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NATURAL SELECTION AND ADAPTATION

Papers read at the
Annual General Meeting of the Society
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NATURAL SELECTION AND ADAPTATION

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THE DARWINIAN AND MODERN CONCEPTIONS OF NATURAL SELECTION

H. J. MULLER

Professor of Zoology, Indiana University

(Read April 21, 1949, in the Symposium on Natural Selection and Adaptation)

DARWIN'S theory of evolution through natural selection was undoubtedly the most revolutionary theory of all time. It surpassed even the astronomical revolution ushered in by Copernicus in the significance of its implications for our understanding of the nature of the universe and of our place and role in it. Surely, the most miraculous seeming phenomena in existence are the superlatively intricate organizations of plants and animals (including ourselves), with their manifold complications all directed, as if by design, towards an end—that of perpetuating their own kind.

Even the general idea of evolution, shared by not a few before Darwin, did not help, fundamentally, to explain how this result had been attained. For so long as evolution was thought to be guided chiefly by an internal perfecting principle, or by the direct action of external conditions, or by the inheritance of adaptive effects of use, principles all of which were advocated by Lamarck, men were no nearer a real solution of what caused the changes to form a working system that was for the organism's benefit. In lieu of an explanation, in fact, they started out by assuming the prior existence of the main thing to be explained, namely, design, but they assumed its existence in a generalized and insubstantial form that was even more miraculous than the specific forms in which, on this view, it finally crystallized. Thus it remained for Darwin—and independently although in lesser degree Wallace—to provide the only possible scientific interpretation, that of the natural selection of essentially blind variations. Moreover, Darwin's masterly marshalling of the evidence for this, and his keen-sighted development of many of its myriad facets, remain to this day an intellectual monument that is unsurpassed in the history of human thought.

It is true that Darwin did defer to past views enough to accept to some extent the ideas of directive change of heredity by "definite" environmental "effects on the reproductive system," as he termed them, and by the inheritance of effects of use and disuse. But he pointed out that these supposed processes would be insufficient by themselves to explain the origin of adaptations in general. And he showed that, in many kinds of cases, as in neuter insects and in numerous ecological adaptations, natural selection by itself must have achieved the whole of the remarkable organization found. It is also true that a few others before Darwin and Wallace, going back at least as far as Empedocles and Aristotle, had occasionally had glimpses of the idea of natural selection. So did, in a much more cogent and modern way, Dr. W. C. Wells, originally of Charleston, S. C., in 1813.[1] But all these forerunners had only applied this notion in a very limited manner, or to a limited group of organisms, and had missed the chance of elaborating upon how it served as the grand clue to the whole system of developments.

The word Darwinism, then, should rightly connote *the* distinctive contribution of Darwin and Wallace—natural selection as the key to evolution in general. This contribution stands not merely unimpaired today, but corroborated and implemented in innumerable ways. It is curious however that, on the official and compulsory Soviet view, Darwinism means everything except this: that is, it means everything that Darwin had grudgingly borrowed from pre-Darwinian times. Natural selection, in so far as it means the supplanting of one kind of individual by another of the same species—and in this intra-specific competition Darwin as well as modern students of the subject see its chief means of operation—is explicitly denied on this anachronistic version of Lamarckism, which uses Darwin's name.

It is unfortunate that Herbert Spencer proposed the expression "survival of the fittest" for Darwin's very apt term "natural selection," and that Spencer's expression was accepted even by Darwin himself, as well as by many others, as equivalent to Darwin's own. For the word "fittest" in Spencer's phrase can only be properly

[1] See R. H. Shryock, The strange case of Wells' theory of natural selection, in *Studies and essays in the history of science and learning in honor of George Sarton*, 1946, also C. Zirkle, Natural selection before the origin of species, *Proc. Amer. Philos. Soc.* **84**: 71–123, 1941, and C. A. Kofoid, An American pioneer in science, *Sci. Mo.* **57**: 77–80, 1943.

defined as meaning: "having such a character as better to survive." Thus his expression, taken literally, must be translated as reading: "the survival of those which survive." This tautological form has led people into philosophical muddles and has caused them even to question the validity of the entire concept. However, the underlying idea is of course not "the survival of the survivors," nor in fact, mere survival in itself. It is the principle that there is, in the first place, *heritable* variation in *different directions,* and that this is followed by *differential* survival *and multiplication* of the variants. We might abridge it all more accurately by terming this "the differential multiplication of diverse variations," but "natural selection" is terser. Moreover, Darwin's own term is the more explanatory, because it calls to mind the analogous and more familiar process of artificial selection. In both the terms natural and artificial selection, after the tacit assumption has been made that the variants can be multiplied *as such,* the emphasis is on a wide range of choice for this multiplication process. For without this diversity of material the term "selection" would be meaningless. The adaptiveness of the products of evolution follows this, as a necessary consequence of this wide range of natural choice, and so the process as a whole is quite appropriately called "natural selection."

Of course all matter, inanimate as well as animate, is to some extent subject to variations of diverse kinds, some more conducive to survival than others. But what makes living matter so uniquely subject to indefinitely accumulated evolutionary accretions is the fact that its variations are, as we say, heritable, which really means that they can be multiplied. They have to be multiplied differentially because, as Malthus and following him Darwin pointed out, there is obviously far too little room and means of subsistence for all descendants, i.e., there is a "struggle for existence." But if there were infinite room and means of subsistence, and if all descendants could somehow be kept alive, still the very fact of the multiplication of diverse variations, without its being differential, would eventually result in the stepwise origination of all the forms of life we have today.[2] However, in that case the forms corresponding to our living ones, though in absolute numbers as great as today, would be so vanishingly few, relatively to the total, as to be lost in it. For that total, including all the conceivable "misfits," would be so stupendous as not to be containable in a universe of universes.

An indefinitely continued and quite unrestricted multiplication of variations, then, would in the end, through the sheer numbers attained, give opportunity for the most improbable of all arrangements, namely, complexly working adaptive organizations like ourselves, to come into existence without design. They represent however the almost infinitely rare, the most select, combinations of chances. *Differential* multiplication, with its struggle for existence, allows these to be generated practically in this imperfect world, despite its physical limitation of room, and in fact as if there were infinite room for them, by eliminating those others which would stand in their way and simply giving reign to their own natural powers of multiplication and further variation. If those who found it inconceivable that such complicated organizations could arise by a succession of "chance events" would take the trouble to reckon what an infinitesimal proportion of the total number of trials made in an unrestricted multiplication process these successes represent, they would arrive at a figure so staggeringly minute as to be quite commensurate with their quality, as I have pointed out on a previous occasion.[3]

The one great requisite for all this is the possession by living matter of the property of *multiplying its variations.* It is just this which, on our view, most fundamentally distinguishes living matter from non-living. And it is this which distinguishes what we now recognize as the gene, whether it lies in the chromosome or elsewhere, from the rest of living matter. This makes the gene prior and basic, and makes the rest of living matter only a complex resultant, which arose as a series of by-products of the genes' variations that happened to be useful in furthering the multi-

[2] We neglect here the selective influence of elimination in restricting the process of intercrossing, and in thus leading to a concentration of different adaptive variations within particular lines of descent.

[3] The argument in this and the preceding paragraph was set forth in greater detail in the author's paper, The method of evolution, *Sci. Mo.* **29**: 481–505, 1929. There it was also pointed out that even multiplication is not, theoretically, necessary for the result, if the number of individuals finally reached by multiplication had somehow been provided from the beginning, and if all had simply been kept in existence and allowed to vary in diverse directions with the same frequency and permanency as if they had multiplied. But again, the total number required would be great far beyond all bounds of possibility, and the adaptively organized product would form but an infinitesimal part of this total.

plication of these genes, and hence of the organisms containing them.[4]

In view of this evolutionary mechanism it is semantically confused to dispute as to whether natural selection is "creative," for the answer depends only on our definition of that word. We have just seen that if selection could be somehow dispensed with, so that all variants survived and multiplied, the higher forms would nevertheless have arisen. This shows that the *vis a tergo* here is not selection but diverse variation and the multiplication of variations. Yet in actuality this situation is impossible, and so it is selective elimination which gives the conditions under which the "fitter," and they alone, can really assume their shapes. This process is far more "creative" than the pruning of a tree, to which it has sometimes been compared, and more creative even than the whittling of wood from a block to form an image which, among an infinite number of other potential images, had, in a sense, lain latent within the block. If this is not actual creation, then no sculptor creates his statues, and no poet, in selecting his particular words out of an almost infinite number of possible combinations, creates his verses.

As providing the diverse range of material needed for natural selection, Darwin laid emphasis upon what he called "individual variations," which he regarded as being produced by the "indefinite effects," as he put it, of external conditions acting "upon the reproductive system" in no directive way. He regarded the production of these variations, unlike that of the supposed "definite effects" previously referred to, as governed by the operation of "chance" factors, which at bottom, however, were subject to natural law. These indefinite effects, according to him, embraced most of the differences, of varying size but usually small, distinguishing individuals of the same population. Darwin also recognized non-inheritable differences, but said that he was not concerned with them. That most of the inheritable individual differences were not directively induced by given conditions of the general environment he considered evidenced by the fact that the same kinds so often occurred under different kinds of environment, and by the converse fact that different kinds occurred under the same kind of environment.

[4] This was pointed out in the author's paper, Variation due to change in the individual gene, *Amer. Nat.* **56**: 32–50, 1922. Timoféef-Ressovsky has termed this process "convariant reproduction."

As previously stated, however, Darwin believed that there were also directed, or as he called them "definite" heritable variations, caused by particular types of changes in conditions. These variations on his view tended to make the population as a whole vary in a given direction, but he ascribed to them a minor role. Not presenting a wide range of choice, they could not solve the general problem of adaptation. Along with such definite variations we might here include also characters acquired by use and disuse if, as Darwin thought, they might be inherited.

Modern genetics has substantiated and intensified Darwin's main conclusion concerning the variations that furnish material for evolution. Studies of spontaneous and induced gene mutations have shown the practical independence of the types that occur from the kinds of environmental conditions prevailing, even in bacteria. This is certainly true so far as any directive effect of environment on evolution is concerned. There is also evidence that, under any known conditions, the adaptive mutations form an exceedingly small minority of them all, as would be expected on a chance relationship of adaptive effect to type of condition. The manner of variation of their total frequency with the amount of thermal agitation and of radiation present, and the relative indiscriminancy with which the different genes are affected by such chemical agents as are known to be mutagenic, are telling facts in this connection. They demonstrate that mutations, in general, have their basis in ultra-microscopic accidents occurring on a molecular and sub-molecular level, and that the amount and form of energy required for the different gene mutations are very similar. Thus Darwin's so-called "indefinite" effects of environment on individual variation are not only proved to exist but made in a general way understandable, in terms of our modern knowledge of the finer structure and behavior of matter. It thus becomes clear that the nature of the gross environmental conditions, such as climate, food, or opportunity for exercise of this or that type, is of little or no practical importance in the origination of the so-called "indefinite" variations.

At the same time careful study has shown, in all cases well analyzed, the non-existence of the "definite" or the directive type of inheritable change in the individual gene. We need except here only some cases of abnormal, so-called "mutable genes," but these are now suspected of involving atypical chromosome breakage and

union of pieces, and they are in no sense to be considered as adaptive to the special conditions that produce them. Moreover, unlike what Darwin thought, even a *change* of a given kind in environmental conditions is found not to be in itself a cause of the putative variations of "definite" types, i.e., of variations in a prevailing direction, different from the direction otherwise found. In believing that this phenomenon does exist, Darwin had been misled by the increased number of deviant individuals or varieties of particular kinds found under changed conditions, although he himself had warned of the difficulty of distinguishing between the effects of selection, in giving such results, and effects due to differences in the process of variation itself.

As for the inheritance, from one generation of multicellular individuals to another, of characters acquired by the somatic tissues, this group of readers need not be told that, with the passing decades, more and more evidence has accumulated against the existence of any such process in nature. This generalization is not threatened by the occasional cases of transmission, through the germ cells, of micro-organisms, viruses, or other gene-containing bodies or genes, that can be acquired by some sort of infection. For no general mechanism for the inheritance of adaptive somatic modifications is thereby provided. The same stricture applies for the "plasmagene" and "plastogene" types of inheritance that have been found in some micro-organisms and throughout the plant kingdom.

There used to be much argumentation as to whether the main material for natural selection was furnished by so-called "continuous variations," or by "discontinuous" ones, and for a time the latter were identified with the "mutations" of de Vries. Darwin actually made no sharp distinction here, but realized that there are all degrees of change, with the larger steps, especially those giving distinct abnormalities, the rarer. And he held that the very large steps were much less likely to be advantageous, and so to furnish favorable material for natural selection. In this matter we now stand much closer to the view of Darwin than to that of de Vries. This despite the fact that our modern knowledge of the small steps of individual variation proves them to be mixtures, individually almost unravellable, of small mutational differences with continuous, non-inheritable somatic modifications.

We have evidence that, in general, mutations giving small phenotypic changes arise more frequently than those giving large ones. It is also clear that the large changes are on the average correspondingly more disadvantageous. Moreover, crosses between varieties or species show that tiny steps, occurring in multiple factor systems, usually form the basis of the observed differences between the groups, especially where these differences themselves are relatively large.

With Darwin we believe that the greater disadvantageousness of a larger change, in cases in which the main feature of such a change is advantageous in its direction and even in its magnitude, if considered by itself, is due to the correlation of other characters with the primary one. This works out in two ways. First, a mutation causing a more drastic change in one character is apt to entail, at the same time, larger and on the whole more harmful changes in other characters as well. Second, the large change in the primary character, even if it would, when able to function adequately, be more advantageous than a smaller one, meets with the difficulty of finding itself with a system of coexisting characters that have not yet been brought up to its level, so to speak. An example of the latter relation would be a case in which larger size appeared without the disproportionately larger muscle and bone cross-section, and the more pillar-like leg structure, required to support and move the increased mass. For the above two reasons, then, most selected steps will be small. And the taking of many small steps in the same direction by a given character will be deferred, to allow the correlatively necessary steps in other features to be taken, virtually *pari passu*. As for the relatively few large mutational steps allowed to gain a foothold, these will have to become elaborately "buffered," as Julian Huxley terms it, by small "modifying" mutations that take care of their disadvantages, before evolution can proceed again in the same direction. Thus evolution is caused to move slowly and for a long time in a given direction, as Darwin pointed out. And the effect was seen by him to be one of selection—or as it has recently been termed, "orthoselection"—rather than of "orthogenesis" in any of its older meanings.

Of course, as he also saw, there is often a further reason for such continued change in one direction, lying in the fact that the environmental conditions to which the organism is adjusting may themselves continue to change in a given direction. This is especially true when some character or group of characters of other organ-

isms, which are undergoing their own evolution, constitute the key environmental condition for the organism primarily in question. Sometimes indeed this relation is mutual, the changes in the "primary" organism giving by reaction changes in the others which then react back upon the first organism and so, step by counter-step, through ecological channels, result in a long drawn out evolutionary chase. An example of this is seen in the parallel increases in the wearability of mammalian teeth and in the silica content of vegetation; another is seen in cases of mimicry in which the mimicked type tends to become selected away from the mimicking while the latter follows after. None of this gradual evolution is opposed to modern mutation theory but, on the contrary, it is to be expected on it.

In line with this emphasis on small steps it is increasingly found that, as Darwin had thought, even small differences are of importance in survival. So much is this the case that, as modern genetics has discovered, selection has brought into being morphogenetic and physiological systems that give a high stability of development to the characters of organisms in the face of varying outer conditions which would, but for these special regulating mechanisms, cause much more considerable fluctuations in them. In part, this stabilization has been accomplished by increasing the potencies of the genes more primarily concerned with a given character to a near-saturation level, while keeping their final effects down to the optimal through groups of "modifying genes." Pertinent evidence for this conclusion has been obtained by studies on the effects of changes in gene dosage and on the peculiar dosage-compensation mechanisms possessed by sex-linked genes. The high grade of dominance exhibited by most normal genes over their mutant alleles appears to be merely a by-product of this more general stability. Moreover, as the dosage-compensation work more especially shows, the degree of stabilization thus achieved is often such as to prevent deviations of development far smaller than could be detected by our unaided eyes. This result shows that even changes which to us seem sublimal are nevertheless important for survival, and furnish material for the operation of natural selection.

Darwin thought that high stability, both with regard to varietal and specific characters, resulted in some automatic way from long continued selection for a given grade of the character. He also thought that, in other cases, characters of no particular use served as good systematic marks merely because of a low intrinsic variability. Geneticists today would look with skepticism upon both of these views. Instead, they would interpret the greater stability of given characters as being usually due to an actual selection of such genes as produce somatic reactions especially resistant to disturbing influences, and even reactions of a self-regulatory ("cybernetic") type. It is here implied that all these characters, including the systematic ones, are in some manner useful. Of course characters that have been longer selected for are correspondingly better guarded in these ways, both from the effects of varying environment and of mutant genes. Conversely, there is a relatively high variability on the part of newly established characters, and more especially of mutant characters not yet established at all. At the same time, we also recognize that intrinsic variability itself is subject to modification by selection. This occurs, on a piecemeal scale, by the replacement of more mutable genes by stabler alleles. Much more important, however, are the effects produced by the natural selection of genes, and genetic systems, that favor a lower or a higher general mutability (as the case may be), in adaptation to the needs of the species.

Now while the stable development of a character in relation to most environmental disturbances is on the whole a great advantage, there are innumerable special cases in which it is more useful to have a character change in a given way in the presence of a particular kind of alteration of the surroundings. In many of these cases, particularly if the environmental change in question is a frequently occurring one, adaptive developmental or physiological reactions have been evolved by selection, providing the appropriate response, as is to be expected. In fact, the whole fabric of a living thing, with its "adjustment of internal to external conditions," in such a manner as to favor perpetuation and multiplication, is a system of just such reactions. This has often fooled the Lamarckian by confronting him with adaptive morphogenetic processes, such as the growth of a muscle accompanying its use, which, being *results* of evolution, he has mistaken for its causes. There can be little doubt that many of the laws of heterogonic growth, such as those determining the shapes of ant castes, or the overgrowth observed in some of the bony and horny structures of larger reptiles and mammals, as well as such principles as Gloger's rule, belong in this

category. In line with this, as Darwin recognized, the rules of correlative development are not themselves immutable, but can be modified or even overcome by variation and selection. In fact, plenty of examples of the breaking of the rules are known.

We would, however, go beyond Darwin in applying the above principles, and maintain that few if any widespread, long-lasting characters of the adult are to be explained away, in the manner proposed by him, as secondary effects of a selection that had really acted only on certain more important characters, with which the ones in question had merely been correlated in their developmental mechanism. For the evidence concerning the importance for survival of even apparently minor differences indicates that they would not ordinarily be carried along passively in the evolutionary current. Their developmental correlation, unless giving a beneficial result in the given instance, would in most cases be compensated for by appropriate mutations affecting them separately, if enough time were allowed. On the other hand relatively newly established characters and, still more, mutations that are not established, must often entail developmental correlations that are not advantageous, or that are distinctly disadvantageous. So also must unusual environmental conditions, for which the species has been insufficiently or not at all selected. Included in the latter category are conditions created by a more efficiently evolving competing organism, such as a parasite whose genes have evolved so as to produce in the host a gall adapted to itself, but damaging to the host.

It would take us too far afield here to consider in detail the factors affecting evolutionary speed or direction. Modern students of evolution agree with Darwin that selection must work to alter the species more rapidly when conditions of importance for the organism have changed, and that among the most influential of such changes are those in other species, in relation to which the organism becomes adjusted. The opening up of new ecological niches for the organism, as well as its immigration into other territory, is usually associated with significant alterations in the physical and organic conditions of its existence. As before noted, however, we do not follow Darwin in believing also that outer changes tend, *per se*, to increase, to an extent significant for evolution, the genetic variability, nor is this necessary for the result.

Sometimes following in consequence of the outer changes which alter the course of selection, but also capable, theoretically, of occurring without them, is the evolutionary origination, within the organism, of "innovations" that alter its mode of life, either qualitatively or in a radical quantitative manner. These inner changes themselves can in turn react to alter the course and speed of the further selection. As Darwin reiterates, while variations are common, innovations are rare. The distinction between the two categories remains a valid one, even though there is no sharp line between them, and although we must follow Darwin in inferring that the innovations themselves have usually arisen by slow degrees, through the cumulation of minor variations that are not, individually, to be regarded as innovations. However, in some cases, especially in those involving change in function, to which Darwin calls attention, the inwardly conditioned change in some important aspect of living may have been a relatively sharp one. Now the innovation, whether sudden or gradual in its onset, will tend to usher in a period of rapid change by selection, as it becomes improved and other characters become altered to suit it. Occasionally, broad new avenues to survival and multiplication are opened up thereby, and in such cases opportunities are apt to arise in a number of different directions, all new for the organism. Thus in addition to the "spurt," or acceleration in evolutionary speed, there may be a kind of "burst" of diversification or, as Osborn called it, "adaptive radiation." Gradually, however, new limits, temporary or permanent, are approached, and the evolutionary movement becomes slowed down again in both its length and breadth.

On this view, there is no cogent reason for regarding those great groups which have long ceased undergoing important evolutionary changes as being intrinsically less variable than the others. We might however grant that a selection of genes which reduced the mutation frequency would be favored in them, provided even short-range changes in conditions, of a sort that rendered temporary genetic alterations useful, had largely ceased to exist for these organisms. Such a contingency would seem rare, however. And, in any case, their stasis would, primarily, have been caused by the fact that they had reached a blind end of selection, an "optimum" for any mode of life presently attainable to them.[5] This would be

[5] The "optimum" is of course only relative to the possibilities more immediately around it. It presents an analogy to the relatively stable state reached in chemical

because of limitations in the advantages of further developments in their own characteristic structures, taken in relation with the fact that they were hemmed into their own niches by other organisms, which hopelessly outdistanced them for other possible fields of conquest. Thus, although changes in them could still occur, there would be virtually no important ones that presented long-term advantages.

But even though organisms may have reached a virtual stopping point in evolution, the mere maintenance of their present structure requires, as we realize today, the persistent operation of natural selection. Darwin, to be sure, stated that a relaxation of selection leads to an increased accumulation of individual variants. But in his time the knowledge was apparently lacking that the relaxation of selection with regard to any character would lead to decay down to the level at which selection does operate, and that an actual cessation of selection for a character would in time lead to its complete disappearance. In fact, the entire organization would deteriorate similarly, if selection in all directions were relaxed. Before the advent of modern mutation study, it was not known that genetic changes in the downhill direction are in general far more frequent than those which increase or intensify an organ or character. True, Darwin was so astute as to point out that such a principle, if true, would be of great service in explaining the reason for the decline, and more especially for the total disappearance, of features which had lost their usefulness, like the eyes and the pigmentation of cave forms. Today however this principle is accepted by geneticists. And it gives a new importance to natural selection, as a process which not only leads, sometimes, no further adaptations but which is everywhere actively at work in maintaining all things biological that merely continue in existence.

As to the forms which natural selection can take, we can enter into no adequate discussion here. Sexual selection is of course only one kind —in fact, it includes several kinds—of natural selection, and modern geneticists are not inclined to share that doubt of it which actuated many biologists of the older generation. They might, rather, raise the question more actively as to how that more basic natural selection had worked which established and maintained the particular characters through which the given sexual selection itself operated.

It is to be noted that there are usually more or less conflicting kinds and currents of selection at work together. Most characters of a complex organism, living in complex surroundings, are advantageous under some circumstances or in some of their relationships and to some extent disadvantageous under others. Moreover, we may distinguish between advantages of longer or shorter duration, and, correspondingly, between longer- and shorter-term selection. Related to these problems are those of intra-group and inter-group selection, processes which often are opposed in their direction. The final outcome then must be a resultant of the combined action of the various selective tendencies.

Sometimes, however, instead of a compromise, an enduring dimorphism or polymorphism is attained, as in the establishment of separate sexes, of neuters, and of other specialized divisions of the species. It would be interesting to examine the evolutionary mechanisms involved in such cases, in the light of modern genetics, had we the time. Suffice it here to say only that in each case in which the different individuals are able to breed independently of one another (as in polymorphic butterflies), a stable equilibrium is necessarily involved. This is so constituted that a diminution of numbers of a given type puts a higher premium on just that type while, conversely, a rise in its frequency above the equilibrium level leads to its lowered survival, so that in either case the balance is again restored.

Darwin, unlike many of his followers, recognized that the resultant of selection is not always for the ultimate profit of a species. In particular,

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combinations that have a lower "potential energy" level (higher entropy) than those from which and into which they can readily be transformed. Such structures therefore tend to remain as they are despite the fact that other combinations of their parts, with still lower energy level, are possible. To jump the surrounding energy wall and attain another low level, an unusually large amount of energy must first be supplied. Similarly, for the organism to escape from its selective dead-end, the radical jolt in its mode of living brought about by a significant outer change or inner innovation becomes necessary. There are of course all degrees of this phenomenon. Wright has graphically described the same phenomenon by analogy with troughs, peaks, and other changes in the contour of a surface over which an object may move. In this case also the analogy is to energy levels. It is important to remember, however, that in the evolutionary situation we are not dealing with differences in actual energy, in the physicists' sense. For the steps in our case are steps of differential multiplication of such a kind as to result in increasing organization, and no more transfer of energy need be involved when the multiplication is differential in this way than when it is differential in some other way or not differential at all.

he drew attention to the problem of characters which benefit the group without being of greater advantage (and sometimes being of actually lesser advantage) to the individual himself and his own descendants than to the rest of the group. Such characters are, for instance, the sting of the bee, which causes its own death, and (under some circumstances at least) breadth of sympathy in a man, which may handicap his own and his children's struggle for existence. Characters which are useful only to the group as a whole cannot be selected for except by means of an inter-group biological competition between numerous small groups which fail to interbreed freely. The converse of these social characters are those which are actively selected for in intra-group competition but which work to the whole group's detriment. The counteracting of the latter process, in nature, also requires inter-group selection. As Darwin realized, such inter-group selection is now much diminished, if not absent or even reversed in its direction, in civilized man. So also is that intra-group biological competition which tended to lead to the survival of those who were physically and mentally strongest. And although Darwin did not realize that a mere absence of selection above any given level would inevitably lead to biological degeneration all the way down to that level, he did call attention to the danger, in civilized mankind, of reversed selection. In his day, however, scientific techniques of control over reproduction had not yet been devised, and so he saw little hope of mitigating an evolutionary decline except the admittedly unlikely one of voluntary restriction of marriages.

Our discussion is intentionally concerned mainly with those topics regarding natural selection which were taken up by Darwin, in order that we may assess the extent to which we still agree or disagree with his conclusions. At the same time, it should be realized that our modern knowledge of the genetic mechanism in its varied forms, of mutation rates, gene flux, chromosome changes, breeding systems, population dynamics, etc., allows us to go far beyond Darwin in our understanding of the details of the evolutionary process, and of the qualitative as well as quantitative interrelations of the factors concerned. But Wright's magnificant quantitative treatment must be left to Wright himself, nor can we do more than mention the names of Fisher, Haldane, and Hogben, which are likewise classical in this connection. All of them, however, as I think they would agree, serve to make far more definite, and to implement, the fundamentals of that theory of natural selection which Darwin and Wallace conceived, as it were, at a distance.

What has made all this possible is, first of all, the proof of the particulate or (in the older sense of the term) the "atomic" character of the hereditary material; second, of the precise rules of transmission of these particles; third, the information concerning their phenotypic interrelations, as in dominance, pleiotropy, and multiple-factor cases; and fourth, the evidence as to the quantum character of their changes, together with some data on the frequency of changes of different types. Thus evolution study from the standpoint of genetics has risen to a higher level or, more correctly speaking, has bored down to a deeper level of analysis, and in consequence is also able to make more far-reaching and reliable deductions and integrations.

At the same time, it is worth noting that Darwin's general conclusions regarding selection do not stand or fall according to this or that genetic mechanism, if only we admit the existence of heritable change in numerous directions, or, in other words, the differential multiplication of diverse variations. So, for example, even if inheritance were perfectly blending, the selected individual variations would not in time become completely swamped out as some have maintained and as even Darwin seemed to suspect. Their increment, established by one generation of natural selection, would not be lost but would be duly added to the species, in each succeeding generation to be reenforced by the additional selection. Thus the mean would progress as rapidly as with selection of a dominant gene which goes in full strength to half the progeny. Of course, the variance due to freshly arisen inheritable variations would on this view have to be much greater than that supplied by new mutations in the genetic scheme recognized today, but it would by no means be as great as the observed variance and, more important, it would not be necessary to postulate that quantitative variation in a favorable direction exceeded or even equalled that in the opposite direction. But the rate of establishment of rare, qualitatively peculiar variations would be very slow.

Another claim—in the present writer's view fallacious—that is sometimes made for the superior evolutionary worth of the genetic mechanism known to us, has to do with the supposed advantage for evolution conferred by the recessiveness of most mutant genes. For this, it is said, leads

the species to accumulate a large reserve of hidden recessives, which may be drawn upon in case of need arising from a change of conditions, and which can then enter into varied combinations. The thing that is forgotten here is that the frequency with which a completely recessive gene shows itself at any given time is, on the average, only equal to the frequency of mutation, per generation, to the given gene, multiplied by the average number of generations during which it is allowed to express itself before it is eliminated by selection. And the number of individuals showing it would be just the same, for a gene having a given frequency of origination and a given survival value, no matter whether this gene expressed itself fully and immediately in every individual carrying it, as it would in a haploid species, or whether it expressed itself as a recessive in a diploid species. In fact, be it noted, the rate of increase of individuals expressing a recessive (or on the whole recessive) gene is actually slowed very considerably in an ordinary diploid species as compared with a haploid, when selection acts in the gene's favor. This is because of the circumstance that so small a proportion of the recessive genes are expressed in the diploid individuals which contain them and that selection is therefore greatly restricted in the force of its operation on them. This lag in selection may sometimes be of real value, however, not for the mistaken reason sometimes given that a short-term selection is aided by the phenomenon of recessivity, but rather for the opposite reason, namely, that it acts as a damper to prevent a merely temporary selection from altering the population too hastily and so doing long-term damage greater than the short-term good.

Another fact in regard to recessivity and dominance which will call for revision of some modern treatments is the assumption so often made of the usual completeness of dominance. There are a number of lines of evidence, not well enough known, derived from dosage and dosage-compensation studies as well as from direct tests, which indicate that most so-called recessive genes do have some degree of expression in the heterozygote, and that although this is usually below the threshold for our ordinary observation, nevertheless the effect is after all significant for survival.[6] This being the case, many of our calculations concerning selection should take much more account than they do of heterozygous individuals. When they do this, they will assume a form which is in some respects a good deal simpler than now, for selection is thereby made more direct, and nearer to the kind of process envisioned by Darwin.

On the other hand, the genetic knowledge of Darwin's day was too primitive to allow him to have a good comprehension of the role of sexual reproduction in relation to evolution, although Galton had noted that recombination types can be formed in subsequent generations, and had based a mosaic conception of heredity upon it, and Weismann's ideas of panmixia and of chromosomal inheritance approached somewhat nearer still to the truth as we now see it. Today we recognize that the basic function of sexual reproduction is an out-and-out evolutionary one, pure and simple: namely, that of allowing, through the processes of crossing over and of random assortment of chromosomes, the simultaneous differential multiplication of diverse independently occurring variations which otherwise would have to compete. They are thus allowed to form combinations, even though they had usually originated in different lines of ascent, and the process of their accumulation by selection is inordinately speeded beyond what it would be if, as in asexual forms, the different selected mutations which it was advantageous to have in combination had to wait until they arose successively within the same reproductively isolated line. This advantage is further heightened by the fact that the genes entering into some of these favorable combinations are useful only, or mainly, when in that combination, for these would have had still less chance to gain a foothold by the procedure of single-file origination and selection.

We have not yet touched upon the topics of the influence of population size and population division upon selection. It does not seem to be widely realized that these are themes which Darwin by no means neglected, and that, in fact, he came remarkably near to some of our most important modern conclusions concerning them.

[6] For further treatment of this matter see the following papers by the present author: Evidence of the precision of genetic adaptation, in the volume of *Harvey Lectures* for 1948, p. 165–229 (publ. 1949); Some present problems in the genetic effects of radiation, in press, Oak Ridge Symposium on Radiation Cytogenetics, Apr., 1948, *Jour. Cell. & Comp. Physiol.*, supp. vol.; H. J. Muller and S. L. Campbell, Further evidence that most "recessive" genes exert their main action as dominants, (in press) 1950. Direct evidence on the matter was furnished by C. Stern and E. Novitski in their paper, The viability of individuals heterozygous for recessive lethals, *Science*, **108**: 538–539, 1948; this paper had, however, not come to the present author's attention when the above was written.

For one thing, he recognized that large populations, by providing a greater absolute number of rare variants of diverse types, afford richer material for selection than small ones. However, he could not know how important the infrequent accidental processes are which enter into the obtaining of a foothold for advantageous rare variants, or variant combinations, especially if they be recessives, and so he could hardly grasp the force of this point as well as we do. For the rarer an accident is the more are large numbers necessary to achieve its realization. Moreover, in just this kind of case the non-swamping of the rare variations, caused by the non-contamination of alleles by each other, assumes especial importance in giving them value, as previously mentioned in our discussion of swamping effects, and this too is a property of them that was unknown to Darwin.

Secondly, Darwin recognized that the dispersal of a population over a wide area, by bringing it into contact with diverse conditions of selection and so leading it to form local varieties or races, was an aid in evolution. He saw these varieties often competing with one another later, and so—again by offering more diversified material for selection, but this time on the varietal level—achieving a success for the species as a whole which surpassed that of a completely panmictic population of equal size. The species small in numbers and/or limited in range, on the other hand, he saw to be more subject to accidental vicissitudes which were likely to exterminate it, and unable in the long run to keep abreast of its larger, more versatile and better insured competitor-species.

Today, thanks especially to the work of Wright, utilizing the facts of modern genetics, these conclusions have been greatly extended and refined upon. The principle of gene "drift," applying more strongly to small populations, increases the divergence of the local groups of the large species. And, through both drift and special local, often temporary, types of selection, some of these semi-isolated groups are carried through the stage of genetic combinations which in the species as a whole would be disadvantageous—situations called "troughs" by Wright. These, however, sometimes serve as stepping stones to unusually advantageous genetic combinations, that could not be attained by a large species subject only to a steady generalized selection. Thus prize local products are formed which may then spread, in more or less fair competition, throughout much or all of the species. Turning now to the small species, we find that it suffers not only from the disadvantages listed by Darwin, but also, if small enough, from the fact that in it there is a considerable drift, which in the great majority of cases will be disadvantageous, and may drag it down despite selection.

In the further evolution of the large widely spread species Darwin saw it tending to split into ever more different types in different places, until they finally ranked as separate species. Like some or most of the geneticists and systematists concerned with evolution today, he thought of the splitting as occurring between groups inhabiting different areas, although sometimes contiguous ones, rather than as occurring in the same area, sympatrically. Related species now inhabiting the same area he regarded as having usually invaded one another's territories since their differentiation, a view for which Ernst Mayr has recently presented cogent arguments. However, since Darwin was not aware of the rules of genetic recombination which, as we see the matter, form the chief block to sympatric speciation, his conclusion had to rest on a less secure theoretical (as well as observational) basis than that of today.

It is interesting to note that Darwin regarded the evolutionary acquirement of what is called physiological or genetic isolation—the inability to cross effectively, in the sense of allowing an interflow of hereditary material between populations—as a mere by-product of an evolutionary divergence that was caused primarily by the selection for other features. To this there must now be added the factor of drift. With this addition, this is the view of the matter which the present author at least has taken so far as the production of inviable or sterile offspring on intercrossing is concerned. Some geneticists however have thought this property to have been acquired by selection, in virtue of the protection against contamination by the other population which such a barrier to mixing affords. In regard to this question, Darwin himself had taken the trouble to point out that the very individuals which possessed this advantageous feature of cross-incompatibility could hardly benefit their descendants thereby and so undergo a selective multiplication. For if they actually tried the crossing, even though it failed to lead to mixture, they would tend in consequence to be checked in their own multiplication. For this reason there could be no effective intra-group selection for this char-

acteristic in itself. While this argument does not appear entirely valid so far as concerns the inability to cross-inseminate or to cross-fertilize, it would seem to hold for the inability to form fertile or viable hybrids. And since, as a matter of fact, this is the kind of block to interchange of hereditary material which often or usually appears first, the conclusion would still stand, for many or most cases, that the physiological isolation was only a by-product of other changes, and not a product of selection for this property itself.

It was long ago asserted by Bateson (1921) that genetics had thrown no light on the problem of how the property of genetic isolation which prevents species from mixing had originated, and this statement has often been repeated by others, mainly by non-geneticists. There have however in the intervening years been many excellent genetic studies of differences which cause considerable genetic isolation between subspecies or species. The groups concerned are nearly enough related to allow some genetic recombination and analysis, when special means are employed, yet far enough apart, either physiologically, ecologically, or geographically, to be practically isolated when in a state of nature. The studies on multicellular animals have agreed in showing that chromosomal genes are responsible for the incompatibilities, and that they give their characteristic isolating effect not singly, but only as a result of differences invoked by given combinations of them. There is no reason to doubt that these genes originated by the same kind of mutation process as the others.

As for plants, much evidence of the same sort has been obtained (chiefly through the findings on sterile hybrids that give fertile tetraploids). In plants and some microorganisms, however, owing to the existence of plastogenes and plasmagenes in addition to those located in the chromosomes, it is found, as is to be expected, that the former sometimes (though by no means always) participate in the causation of the genetic isolation. Nevertheless, the story even in them remains the same in regard to this fundamental feature: that more than one genetic difference exists between any two genetically isolated groups, of such a nature that, to produce the isolation, a minimum of two mutational steps (one of them sometimes in genes located in the cytoplasm) must have taken place. So, for example, in two species of algae of the genus *Acetabularia* studied by Hämmerling, the plastids from one of the species give an inviable combination when present with nuclear genes from the other species. This situation could have arisen only if at least one plastogene mutation and at least one chromosomal gene mutation (though probably more) had occurred—either one in each line or two in one line—since these two species had diverged from their common ancestor.

For the establishment of the differentiating genes which in their given combinations serve as the genetic isolators of their respective populations, it must be inferred that, in the first place, an outwardly enforced physical isolation, essentially of the type of geographical isolation, was necessary. For if the two populations had been allowed to mix during the genesis of their differentiation, then, whichever of the two (or more) differentiating mutations had arisen first, this would have become exchanged, in part, for its allele in the other stock. In that case, the complementary mutation (or mutations) that was necessary for the production of the incompatibility could not have become established, since the lethal or sterilizing action which it had in the cross-combination would have worked against it even in the stock of its origin. If we attempt to avoid this objection by postulating that the genetic isolation depended upon just one gene mutation instead of two or more complementary ones we meet with still greater difficulties. For in that case the one isolating mutation is even sooner wiped out in the stock in which it arises through the killing or sterilizing action which it has when it tries to cross with the individuals of the original type. For these theoretical reasons, then, as well as because of the evidence derived from the genetic study of species differences, it seems necessary to conclude that the genes causing genetic isolation are effective only in combinations, and that, because of this, they usually arise in populations which are separated from one another by outer circumstances, i.e., by geographical or at any rate topographical isolation, as Darwin thought. Moreover, this being the case, it becomes necessary to conclude that the isolating genes were not established by a process of selection which derived its original advantage from the achievement of the isolating effect itself, but were established, in their original local populations at any rate, through their selective value in other respects, or through drift, as the case might be.

The above discussion has touched upon many topics in a very cursory way. This was neces-

sary in view of the very wide yet searching analysis which Darwin made of the whole subject of selection, if we were to follow out our intention of reviewing the conclusions which he reached, and of seeing them in relation to our newer concepts. It is hoped that enough has nevertheless been outlined to show that, meagre though the knowledge of heredity and variation was in Darwin's day, he succeeded in foreshadowing in a most extraordinary way our modern view, which we base upon the solid findings of modern genetics, systematics, and paleontology. We have to be sure travelled far beyond Darwin. And there is now a world of new problems of first rate importance open to students of the subject. But none of these are in contradiction of Darwin's fundamental theory of natural selection, especially when we divest it of the accretions derived from still earlier authors. And his individual contributions on most major points stand, in fact far better vindicated than ever before, as the basis upon which we are building ever higher.

POPULATION STRUCTURE IN EVOLUTION[1]

SEWALL WRIGHT

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FROM our present knowledge of genes, it seems most probable that life and evolution began with the appearance of nucleoprotein molecules endowed with the remarkable capacity for autosynthesis (table 1, I). This obviously required an environment with a richness in organic compounds which could only have been arrived at in the prior absence of life. Evolution would begin with the occurrence of mutations, duplicating as of the new type. Evolution along any single lineage would necessarily consist wholly of a succession of such mutations. From this standpoint it would appear that the prevailing direction would merely have been that toward increasing stability of the molecule. The whole evolutionary process is sometimes treated as if this were all there were to it.

TABLE 1

MAJOR STEPS IN EVOLUTION

I. *The Gene.* Origin as autocatalytic molecule.
  1. Evolution along single lineage by mutation.
  2. Evolution of population of genes.
    Mutation pressure (selection for stability).
    Selection pressure (in synthetic or predatory capacity).
    Ingression from surrounding regions.
  3. Evolution of array of local populations.
    Differential increase and dispersion.

II. *The Cell.* Equational division of assemblage of genes.
  Evolution largely as above but with greater scope.
  Chromosome aberrations supplement gene mutation.
  Selection for mitotic regularity as well as for external adaptation.

III. *The Interbreeding Species.* Cells capable of conjugation and reduction.
  1. Evolution along gene lineages by mutation.
  2. Evolution of species according to population structure.
    A. Uniparental reproduction with occasional conjugation.
      (Selection among recombinant *genotypes.*)
    B. Biparental reproduction with effective panmixia.
      (Selection according to *average effects of alleles.*)
    C. Array of partially isolated populations.
      (Interstrain selection according to *genetic complexes.*)
  3. Evolution of local array of species.

IV. *Species of Multicellular Individuals.*
  Same processes as under III but with greater scope.

The multiplying genes would soon deplete their store of natural resources: amino acids, pentose sugars, purines, pyrimidines, and energy rich substances. As Horowitz has pointed out, mutations that gave the capacity to synthesize depleted substances from precursors, arginine, for example, from citrulline, would have had much more opportunity to duplicate than ones that did not. Predatory genes, capable of breaking down others, would also be at an advantage. Thus selection would make its appearance among gene lineages and would soon take precedence over a mere trend toward stability. To understand the course taken by evolution, it becomes necessary to consider the history of the whole population of genes in a locality (table 1, I-2). The factors governing such a history are statistical: relative rates of mutation, rates of ingress from other localities, but above all the pressure of selection.

Local populations would presumably evolve into symbiotic systems. One gene might synthesize arginine in excess of its needs but be limited in its duplication by lack of methionine, unless near a gene capable of synthesizing this in excess. Different localities might arrive at somewhat different harmonious systems if sufficiently isolated to prevent swamping. If not completely isolated, useful mutations in one would be able in time to reach the others. Especially successful systems would tend to spread over wide areas but not without modification if dispersion proceeded slowly. Here we have evolution at a third level; that of the whole array of local populations, with dependence on the existence of a certain balance between isolation and dispersion (table 1, I-3).

It is evident that the scope of evolution is severely limited as long as the organism is no more than a single large molecule. It seems to require a rather large protein molecule to function

[1] This investigation was aided by a grant from the Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

as an enzyme in a single catalytic process. Symbiosis among such molecules is a poor substitute for permanent assemblage of all necessary metabolic capacities within one organism.

We may surmise then that the second great step in evolution was the assemblage of many genes into one structure, capable of dividing equationally after multiplication has exceeded certain physical limits (table 1, II). For our purpose it is not important whether the chromosome came first and the cell, with gene products (cytoplasm), mediating between the genes and the external environment, came later, or the reverse. In any case, the assemblage of many genes in one organism means an enormous increase in scope.

There is, however, no essential change in the mechanism of evolution. Mutations may occur at each of many loci and chromosome aberrations may occur involving many loci at once, but evolution in retrospect along any lineage is still merely a succession of mutations. There would also be evolution of local populations, guided in this case by selection for internal adaptation (e.g., perfection of mitosis) as well as by selection for external adaptation in synthetic or predatory capacity. Moreover the rate of evolution of life as a whole would be enhanced by a balance between isolation of local populations and dispersion from one to another. We have essentially the same three aspects listed under evolution of the gene.

Until recently it was thought that all bacteria and blue green algae were representative of this (or a lower) level of evolution. It now appears that in some bacteria at least (Lederberg and Tatum) and even in some viruses (Hershey; Delbruck and Bailey), the third great step has appeared, the possibility of exchange of genes, and recombination. It is indeed possible that occasional conjugation may go back to the origin of the cell and that meiosis was perfected concomitantly with mitosis. It is, however, convenient for purposes of comparison to treat these as separate steps.

With the appearance of even occasional conjugation, evolution along cell lineages virtually ceases. Individual genes still have histories which appear in retrospect as a succession of mutations but each cell lineage becomes merely a short strand in the network-like structure (in space-time) of a larger entity, the interbreeding species. This is the smallest entity above the gene which may be said to evolve (table 1, III.)

The cells with their somewhat limited scope are still the immediate objects of selection. The scope for selection is enormously increased by the appearance of multicellular organisms, which may on this account be considered the fourth great step in evolution (table 1, IV). Reproduction, however, is still cellular. The simplest entity, above the gene, that can be said to evolve is still the species.

The conjugation-reduction cycle enormously amplifies the potential amount of variability from a given number of mutations. Where 100 different mutations in a population in which there is exclusive uniparental reproduction give only 101 genotypes among which selection may operate, the same number (at different loci) in an interbreeding species provide the potentiality for 2^{100} (or more than 10^{30}) different haploid genotypes and 3^{100} (or more than 10^{47}) diploid genotypes. Taking into account the rates at which many mutations are known to occur, the estimates of the number of loci (thousands in higher organisms) and the possibility of multiple alleles at each locus, it would appear that there should be unlimited variability in any moderately numerous species. Actually, most freely interbreeding populations present a sufficiently uniform appearance to be capable of representation, adequate for many purposes, by a single type specimen. There are usually, to be sure, rare variants deviating from the type in the same way as laboratory mutants, and in some cases there is conspicuous polymorphism. These, however, do not seem to present a field of variability at all comparable to that suggested above. On the other hand, it seems to be the rule that all quantitative characters vary and that these variations are in part hereditary. If, as usually seems to be the case, these variations depend on multiple factors each of which has only a very slight effect, the balancing of the effects in individuals keeps apparent variability low even though no two individuals have the same genotype. The field of potential quantitative variability through which the species may work its way without additional mutations may however be enormous. Moreover, compound quantitative variation, beyond a certain threshold, passes into apparent qualitative variation.

In emphasizing the potentialities in a field of multiple minor factor differences, the author has never intended to deny the occasional great importance of more conspicuous unitary differences either in gene effects or chromosome patterns (Wright 1931, 1940 *a, b*). Practically all types

of viable mutational change observed in the laboratory appear to have been involved in the genetic differentiation of species, judging from the results of cytogenetics and from studies of species crosses. Most of these studies, however, indicate that accumulations of vast numbers of unitary changes with individually slight effects have played the predominating role (Dobzhansky; Huxley; Sumner; Baur; Tedin; Harland; Hutchinson, Silow and Stephens; Clausen, Keck and Hiesey; Babcock, etc.).

At this stage in evolution there is a great variety of population structures with advantages and disadvantages, both with respect to current and to phylogenetic adaptation. In some forms, such as bacteria, many protozoa, rotifers, entomostraca, etc., uniparental reproduction is the rule and exchange of genes a relatively rare event. At the opposite extreme, reproduction may be practically exclusively biparental. In either of these cases, there may or may not be effective subdivision into partially isolated populations. There may only be a coarse subdivision into large subspecies, or partial isolation, if only by distance, may occur on such a fine scale that there is statistical differentiation of very small adjacent local populations.

Selection is a very effective process under prevailing uniparental reproduction, provided that conjugation and recombination occur often enough to give sufficient material for it to operate upon. The genotype as a whole, reproduced without change in the clone, is the object of selection.

Under exclusive biparental reproduction and random mating there is more variability since each individual may well have a unique genotype but going with this is the disadvantage that selection can operate only on the average effects of alleles. Genotypes, however successful they may be, are broken up at once by the reduction division. If gene effects were wholly additive with respect to selective value, this selection by mere average gene effect would be no disadvantage but it is clear that interaction effects are very common if not the rule among genes acting on the same character. Moreover the effects of genes are probably never restricted to single characters. Each is so woven into the whole developmental process that additive effects on the selective value of the organism as a whole are exceedingly unlikely. Mathematically, the array of selective values of genotypes must be thought of as a rugged one with multiple peaks (genotypes giving harmonious combinations of characters) separated by valleys. Selection in a random breeding population tends merely to bind the species to one peak, which is not likely to be the highest one.

In a subdivided species, intergroup selection operates, by means of differential growth of local populations and differential migration, on the whole genetic complex which, even more than the single genotype, is the object of selection most directly related to the success of the species as an entity.

As at the preceding stages, one must recognize a third level of action of selection in that among competing, non-interbreeding species. This competition not only has direct effects on the course of evolution within each species but, through extinction and differential rate of speciation, guides the course of evolution of life in general.

The aspect of evolution of the interbreeding species in which statistical consequences of the mechanism of heredity can most easily be analyzed is that of the random breeding population, whether this constitutes the whole species or merely a local, partially isolated race. The elementary evolutionary process here is change of gene frequency. The immediate factors in this process may be put conveniently into three categories, according to degree of determinacy (table 2) (Wright, 1948). First are the systematic pressures of mutation, selection, and immigration which are determinate in principle. Selection pressure, it may be noted, is defined to include

TABLE 2

MODES OF CHANGE OF GENE FREQUENCY (q).

I. *Immediate Change.*
  1. From systematic pressures (Δq determinate in principle.)
     a. Recurrent mutation.
     b. Intrapopulation selection.
     c. Recurrent immigration and crossbreeding.
  2. Fluctuations (δq indeterminate, $\sigma^2_{\delta q}$ and (q) determinate in principle.)
     a. In the systematic pressures.
     b. From accidents of sampling.
  3. From unique events (wholly indeterminate).
     a. Mutation favorable from first.
     b. Unique selective incident.
     c. Unique hybridization.
     d. Swamping by mass immigration.
     e. Unique reduction in numbers.

II. *Secular Change in System of Coefficients.*
  1. From causes within species (control by new peak genotype).
  2. From changes in external environment.
     a. In home territory.
     b. As that of new territory.

exhaustively all processes by which gene frequency may change in a directed fashion without physical change of the hereditary material (mutation) or introduction from without (immigration). It thus includes differential mating, differential fecundity, and differential emigration, as well as differential mortality. In the absence of a secular trend in external conditions, the systematic pressures tend to bring about a state of equilibrium rather than evolution.

Second are the effects of fluctuations in these pressures and of sampling in small populations (Wright, 1931, 1948). These cause deviations in gene frequencies which are indeterminate in direction but determinate in variance. The slight deviations in single generations are compounded by a stochastic process into wide deviations from equilibrium. The probability curve ($\varphi(q)$) describing the distribution of these deviations in single populations in the long run, or describing that among local populations subject to the same conditions, can be deduced from the systematic pressure (Δq) and the variance of the fluctuations ($\sigma^2_{\delta q}$). Thus for one pair of alleles it can be shown that $\varphi(q) = (C/\sigma^2_{\delta q})e^{\int(\Delta q/\sigma^2_{\delta q})dq}$. Formulae can be obtained for multiple alleles and for multiple loci under various assumptions.

The system of coefficients describing the determinate aspects of change of gene frequency may themselves be expected to undergo systematic changes in the course of time. It is convenient to distinguish two major categories: secular changes that trace to processes internal to the species (but not necessarily to the particular local population in question) and ones that reflect secular changes in the environment.

The modes of transformation of a species that is panmictic as a whole and one that is subdivided are compared in table 3. The strong tendency toward equilibrium in a panmictic species, assuming the population to be large, is most readily overcome by secular changes in the external environment It is possible however that a new mutation that is favorable from the first may appear and bring about adjustments in the system of other gene frequencies and thus evolutionary change under constant conditions (Fisher, 1930) but the frequency of such mutations must be very low. If the population is small, stochastic processes may occasionally lead to a new position of equilibrium. In very small completely isolated populations, such processes may, however, be expected to lead merely to random fixation of genes and thus to degeneration and ultimate extinction (Wright, 1931).

TABLE 3

MODES OF TRANSFORMATION OF SPECIES

I. *Panmictic Species.*
  1. Transformation in the absence of secular environmental change.
    a. Systematic response to unique favorable mutation or hybridization.
    b. Shift to control by new adaptive peak after upset by extreme selective incident or extreme temporary reduction in numbers.
    c. Shift to control by new adaptive peak as a result of stochastic processes (small population).
    d. Degeneration from random fixation (very small population).
  2. Systematic response to selection pressure of secular environmental change.

II. *Subdivided Species* (many partially isolated local populations).
  1. Transformation in the absence of secular environmental change by local differences in rates of population growth and dispersion.
    A. Local differentiation in the absence of environmental differences.
      a. Diverse genotypes give same optimum of multiple factor character. Position of optimum fluctuates.
      b. Both homozygotes superior to heterozygote.
      c. Abundance of allele confers advantage.
      d. Responses to local non-recurrent events (favorable mutation etc.)
      e. Stochastic changes in all sufficiently neutral sets of alleles.
    B. Differentiation based on local environmental differences.
  2. Systematic response to secular environmental change, augmented by interpopulation selection.

In a subdivided population with varying sizes and degrees of isolation of local populations, there is much more likelihood of continuing evolution in the absence of secular changes in environment, and also greater capacity to respond rapidly to such changes, than in a homogeneous population of comparable total size. The basis is the differentiation of local populations, for which there are several distinct mechanisms, applying usually to different loci. The most important cause of differentiation is usually no doubt a difference in local environments, the response to which depends on the relation between the selection pressure at each locus and the swamping effect of immigration (Wright, 1931). There may also be differentiation at particular loci in the absence of environmental difference, from selection that favors whichever allele is locally more abundant (Wright and Dobzhansky, 1946) (e.g., genes determining

recognition marks) or that favor homozygotes over heterozygotes (e.g., reciprocal translocations (Wright, 1940, 1941)). All of these have rather more tendency to split the species than to further its evolution as a single group. Fluctuations in conditions that result in fluctuations of the position of the optimum grade of quantitatively varying characters, must inevitably lead to the establishment of different genetic systems, without much character difference, among partially isolated populations (Wright, 1935). This sort of differentiation is of special importance as giving a great store of potential rather than actual variability, easily available whenever extensive systematic change is called for by changing conditions. Next a population may be jolted out of one position of near equilibrium to another by some unpredictable event. This may occur more easily in a small local population than in a large one. Finally the cumulative effects of sampling in sufficiently small and sufficiently isolated local populations may be expected to bring about differentiation at all loci at which the allelic effects are so nearly neutral that selection is not the dominating factor (Wright, 1931). The store of actual, as well as of potential, variability may obviously be expected to be enormously greater in a subdivided species than in a random breeding one of comparable size since different alleles may predominate in different localities, for any of the reasons listed.

These processes are significant for evolution of the species as a whole only as they give rise occasionally to superior *general* adaptations in particular localities. Such an event may be expected to be followed by relatively rapid growth of the population in question, greater than usual outflow of migration and the consequent grading up of adjacent populations. Linkage may be of some significance here. Within a panmictic population, all combinations tend to be formed at random in the long run, irrespective of linkage (Robbins, 1918; Geiringer, 1948). The existence of non-additive selective values (e.g., Ab and aB superior to AB and ab) interferes with this process thereby reducing apparent variability (*cf.* Mather, 1943) but in multiple factor cases in which the selection pressure on each locus is necessarily slight, the interference cannot be great (Wright, 1945). Thus incomplete linkage can rarely be important except for processes in which a few generations are significant. The hanging together of elements of an adaptive complex, during very rapid favoring selection, immediately following immigration may be such a case. Edgar Anderson has stressed this in connection with introgression from one species into another with which it occasionally hybridizes (Anderson, 1949) and it may also be of some importance in intergroup selection within a species.

The importance of population structure in the cleavage of species is more obvious than in connection with gradual transformation as a whole. Table 4 lists the probable major modes of origin of species, classified primarily according to whether the new species arises from one, or more than one, ancestral species. A secondary classification is based on the size of the population from which the new species takes its origin. This may be the whole parent species if there is merely the speciation by transformation, which has already been discussed. There may be splitting into more or less equal components either by a process of gradual transformation of subspecies into species by the development of reproductive isolation or by the extinction of intermediates in a chain of subspecies in which the ends have previously diverged so much that interbreeding does not occur on contact. The number of cases in which the extremes of a circular chain of subspecies live in somewhat different niches in the same locality without interbreeding testifies to the probable importance of this mechanism by which one species may give rise to two without any current genetic change whatever (*cf.* Osgood, 1909; Mayr, 1942).

TABLE 4

MODES OF ORIGIN OF SPECIES

I. *From Single Species.*
   1. Transformation as whole (table 3).
   2. Splitting into more or less equal populations.
      a. Subspeciation followed by selection for reproductive isolation.
      b. Subspeciation along a chain, followed by extinction of intermediates.
   3. Geographical isolation of colony, followed by divergent transformation.
   4. Partially isolating mutation followed by selection for complete reproductive isolation and by divergent transformation.
   5. Autopolyploidy followed by divergent transformation.
   6. Heteroploidy.

II. *From Hybridization.*
   1. Complete fusion of two species.
   2. Introgression into one or both parent species.
   3. Local transformation and isolation of hybrid population.
   4. Amphidiploidy.

In other cases the critical event may be the geographical isolation of a colony which does not differ from the main body of the species to any appreciable extent at the time. Speciation, however, can hardly be said to occur until divergent transformation has brought about consistent character differences and some mode of reproductive isolation that would tend to prevent interbreeding if contact should be reestablished. Such divergence may be expected to occur in the absence of appreciable environmental differences though it would of course be speeded up if differences exist.

Origin of species from single isolating mutations is probably uncommon (in the absence of hybridization). There are, however, probably cases in which autotetraploids, fertile in themselves, but producing almost sterile triploids in crosses with the parent form, have transformed into good species following the isolation (Müntzing, 1936). A partially isolating mutation, such as a reciprocal translocation with semisterile heterozygotes, may constitute a critical step toward speciation if the new pattern becomes locally fixed. This may happen relatively easily if there is the possibility of vegetative multiplication but can hardly occur under exclusive biparental reproduction except where there are many localities in which colonies of the species are continually becoming extinct to be started anew from single gravid females, or at least from very small numbers of migrants (Wright, 1940, 1942).

Hybridization may play a role in the origin of new species in various ways. It may perhaps on occasion lead to complete ultimate fusion of two apparently good species; two species become one. Anderson, as noted above, stresses the importance of introgression of small blocks of genes from one species into another, whereby, if reciprocal, two species give rise to two different ones. With sufficient local isolation, a zone of hybridization between two species with only partially overlapping ranges may lead to the formation of a hybrid species in the region of overlap: two species give rise to three. Finally, amphidiploidy (Winge, Müntzing) may undoubtedly give rise to a well differentiated new species, fertile in itself but producing sterile hybrids with its parent species. This mechanism seems to have been very important in the multiplication of species among flowering plants. Darlington and Moffett have presented cytologic evidence for the importance of heteroploidy either in an autopolyploid or an allopolyploid as an occasional mechanism producing less balanced but nevertheless viable new forms.

The adherents of the view that significant evolutionary steps arise only from single mutations with suitably great effects (Goldschmidt, 1940; Willis, 1940) lay great stress on paleontological and other evidence that seems to indicate an abrupt appearance of higher categories and relatively rapid working down from these to lower categories; and ultimately to species in which further evolution is restricted to mere multiplication of subspecies. It does indeed appear to be the case that evolution is not ordinarily a matter of subspecies tending gradually to become species, these gradually to become genera, these gradually to become families, etc. It is not, however, necessary to postulate mutations of specific, generic, familial, and ordinal rank. A species ordinarily tends to persist for very long periods in a state of equilibrium or at best, very gradual advance under ecological pressures that leave only one restricted niche in which there can be successful competition with other species. Yet such a species may all the time, especially if population structure is favorable, carry a head of steam in the form of a store of potential variability that permits very rapid change (the tachitely of Simpson (1944)) whenever any major ecologic opportunity offers (Wright, 1932, 1941*a*, *b*, 1945). The attainment of a general adaptation superior in a wide range of activities to any hitherto attained or an adaptation that opens up a new way of life may be the end result of a more or less gradual evolution but, once a certain threshold is passed, advance may become explosively rapid if there is a sufficient store of potential variability to draw upon. The same is the case if the species reaches unoccupied territory except that here it is not likely to arrive with a large store of potential variability. However, if a favorable population structure can develop after arrival it probably does not require much time, geologically speaking, to build up an extensive field of potential variability. Even in this case then, the ecologic situation rather than mutation rate is the limiting factor. The contrast between the extensive speciation of the Geospizidae in the Galapagos Islands, in contrast with the lack of such speciation on isolated Cocos as brought back by David Lack, seems to illustrate this point. Drastic alteration of the environment may eliminate many forms and thus give an opportunity for rapid expansion of a form that happens to be preadapted.

Perhaps the most important conclusion from statistical genetics is that neither the driving factor nor the actual limiting factor in evolution is

ordinarily to be sought in the genetic situation (including the process of mutation) once the stage of the interbreeding species of multicellular organisms has been arrived at. The driving force is the universal tendency of life to expand and to seek out all opportunities. The limiting factor in each case is the ecologic pressure from other species and from the non-living environment, by which the species is ordinarily kept in place. The genetic situation in an interbreeding species with a finely divided population structure provides a virtually infinite field of potential variability which permits ready adaptation on the part of the species to fluctuating environmental conditions, ready phylogenetic adaptation to secular changes in conditions, effective exploration by trial and error processes of possibilities of breaking through the restraining pressures even under static conditions, and the rapid exploitation by similar means of any major ecologic opportunity. The result is the observed evolutionary cycle of occasional emergence of a new higher category, adaptive radiation, selective elimination of rival higher categories and return to slow more or less orthogenetic advance and mere multiplication of species, as opportunity becomes restricted to a single channel. A new break through may lead at rare intervals to a new cycle of greater or lesser scope.

The terms emergence and orthogenetic advance are used here, of course, merely as descriptive terms for two contrasting aspects of the evolutionary process not as explanations. It is the contention that the statistical consequences of the varying degrees of success of individual organisms in their efforts to live and reproduce give an adequate explanation for all known major phenomena of evolution when account is taken of the statistical effects of the known processes of heredity in populations of diverse structure.

TABLE 5

THE EVOLUTIONARY CYCLE

I. 1. *Emergence of a Higher Category* (as response to a major ecologic opportunity).
   a. Attainment of an adaptation that opens up an extensive new way of life.
   b. Arrival in territory in which many ecological niches, possible for the form, are unoccupied.
   c. Preadaptation to drastically altered environment, to which rival forms are not adapted.
   2. *Adaptive Radiation* to progressively lower categories.
   3. *Selective Extinction* of rival types.
   4. *Apparent Orthogenesis*
      Restriction to a single possible major line of advance.
   5. *Relative Stability*
      Equilibrium of genus or even species under pressures restricting form to a single ecologic niche.

II. *Rare Emergence of New Higher Category* and initiation of a new cycle at any stage of above. Degree in accordance with that of a new ecologic opportunity.

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SELECTION, "ORTHOGENESIS," AND THE FOSSIL RECORD

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INTRODUCTION

FEW terms in the whole lexicon of natural science have been associated with more meanings than the words "selection" and "orthogenesis." They have been used to symbolize descriptions as well as interpretations of many different kinds of objects, manipulations, and processes, and each has become the sign for several philosophical conjectures which are contradictory and on different or incomparable levels of abstraction.

So many areas of thought are now projected by "selection" and "orthogenesis" that it is customary and necessary for an author to outline the boundaries of factual and other connotations which he implies when he uses either word. This practice has resulted in a large number of personalized definitions and in a host of semantic confusions. It is doubtful whether either word now has precisely the same meaning to any two authors.

One of the most difficult parts of the assignment to write upon the present subject has been the job, while reviewing several hundred articles and books which deal with "natural selection" and "orthogenesis," of trying to learn what various authors mean by these terms. "Selection" and "orthogenesis" are usually discussed in terms of "species" and "evolution," words which have also become surrounded by diversities and confusions of opinion. Poulton remarked nearly half a century ago (1903–1904: lxxvii),[1] in trying to determine the significance of the word "species," that "a word may slowly and unobtrusively change its meaning, becoming, unless critically tested to ascertain whether it still rings true, a danger instead of an aid to clear thinking, a pitfall on the field of controversy." About twenty years earlier, in a discussion of "fossil botany" and evolution, James (1885: 168) had advised that "Wherever the word Evolution comes in, it is well to begin with stating in what sense it is used." Since these dates the literature has expanded enormously and so has the number of senses of the words under discussion herein.

Before conclusions can be drawn about the significance of the fossil record in terms of natural selection and orthogenesis it is necessary to consider some of the former and some of the current meanings of the key words. Their connotations are usually connected with the meaning of "adaptation," but for present purposes the literature about "adaptation," which also abounds with controversy, is not extensively considered although it cannot be completely disregarded in any discussion of evolutionary concepts. This discussion, however, is neither a complete review or synthesis of the literature on "selection" and "orthogenesis," as they have been applied to the study of fossils, nor an effort to place the subjects in a new light by trying to devise new concepts and definitions or to resurrect old and forgotten notions. No attempt has been made to cover the pre-Darwinian literature although many of the more recently expressed conclusions about evolution are probably very old. Zirkle, in his interesting studies upon the history of evolutionary ideas, concluded that Lamarck's hypothesis of the inheritance of acquired characteristics is really pre-Lamarckian by about 2,200 years or may even antedate written records (Zirkle, 1935, 1936, 1946), and that natural selection was described as the cause of adaptation by Empedocles about 400 B.C. (Zirkle, 1941).

Bibliographic references which are cited herein in connection with numerous concepts have been selected not only for their topic pertinence but for their time distribution in the history of ideas about selection and orthogenesis, for their diversity and interest, and for their bibliographies. For these reasons many classic and well known

[1] References in parentheses are to the bibliography at the end of the paper.

and influential writings are not discussed. The brief excerpts, below, are intended to sample the range of opinion from the authors but are not presented as complete key summaries of the authors' ideas. Almost all discussions about evolution are directly or indirectly significant to paleontological studies, and the scattered quotations herein may lead to further attention to some neglected areas in the bibliography on the subject. Many old thoughtful and competent works on natural selection and orthogenesis have been overlooked by recent students.

Miss Marjorie Hindle did much of the bibliographic searching for this paper.

DARWINIAN SELECTION AND ITS CRITICS

Darwin himself, after having defined natural selection or the survival of the fittest as the "preservation of favourable individual differences and variations, and the destruction of those which are injurious" in the sixth edition of the *Origin,* vol. I, p. 98 and reported (I: 99) that several of his contemporaries had misapprehended the term natural selection and that

> Some have even imagined that natural selection induces variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life. No one objects to agriculturalists speaking of the potent effects of man's selection; and in this case the individual differences given by nature, which man for some object selects, must of necessity first occur. Others have objected that the term selection implies conscious choice in the animals which become modified; and it has even been urged that, as plants have no volition, natural selection is not applicable to them! In the literal sense of the word, no doubt, natural selection is a false term; but who ever objected to chemists speaking of the elective affinities of the various elements?—and yet an acid cannot strictly be said to elect the base with which it in preference combines. . . . So again it is difficult to avoid personifying the word Nature; but I mean by Nature, only the aggregate action and product of many natural laws, and by laws the sequence of events as ascertained by us.

Also (I: 98).

> Variations neither useful nor injurious would not be affected by natural selection, and would be left either a fluctuating element, as perhaps we see in certain polymorphic species, or would ultimately become fixed, owing to the nature of the organism and the nature of the conditions.

In a letter to Lyell in 1860 on September 26 (F. Darwin, 1887), Darwin wrote "Talking of 'natural selection'; if I had to commence *de novo,* I would have used 'natural preservation.'"

This comment is of particular significance in view of the recent excellent and provocative discussions of natural selection by Holmes who (1948*a*: 324) points out that it makes a great "difference in one's evaluation of natural selection as an evolutionary factor whether its preservative phase is included in the process."

It is of further interest because some recent authors, in developing their own concepts of natural selection, explicitly deny preservation as an element in the process. For example, Ashley-Montagu (1947: 151) makes the extraordinary statement that natural selection ". . . does not have anything to do with the preservation of the survivors: it is cooperation between the survivors that tends to preserve them."

Darwin's critics have long continued to discover new and ingenious ways of defining natural selection and of perceiving evidences for it or against it. Some have occasionally looked far beyond Darwin's immediate accomplishments and abilities in order to criticize his theory of natural selection. Wheeler (1947: 11) blames poor health for affecting Darwin's judgment of values and speaks also of "the adverse effect of Darwin's temperament upon his grasp of simple phenomena."

There are also many thoughtful and competent treatments of the highly involved history of the term "selection" and its implications in the vast literature on the subject. Fisher (1936: 59–60), while reviewing and criticizing various theories of evolution, in a symposium on the state of the theory of natural selection, comments

> But is it worth considering why, during the three-quarters of a century for which Darwin's views have been known, so many biologists have felt, and raised, objections to them. I believe the explanation must be more temperamental than intellectual. Darwin's work reached a wide public. His views, or something like them, were supposedly familiar to all educated men. That being recognized, few scientific specialists, specialists at least in biology, could suppose that *they* had anything to learn from his works. Even the "Origin," when read at all, would seem to have been read cursorily, without the expectation of learning anything from it. It always seems more knowledgeable to expound the *latest* views, however flimsy.

Whitehead (1948: 114, reprinted from 1925) also criticized the critics of Darwinian selection by saying that "Darwin's own writings are for all

time a model of refusal to go beyond the direct evidence, and of careful retention of every possible hypothesis. But those virtues were not so conspicuous in his followers, and still less in his camp-followers." This observation is in line with Whitehead's conclusion (p. 103) that ". . . in its last twenty years the [nineteenth] century closed with one of the dullest stages of thought since the First Crusade."

A few years earlier Nutting (1921: 129) had observed that

> Two marked tendencies are evident in the history of any important theory after its publication.
>
> First. The followers of the discoverer carry the theory too far and attempt too universal an application. This is manifestly true of Wallace and Weismann who out-Darwined Darwin in their claims for natural selection; of the followers of Mendel, such as Morgan and Pearl; and of many mutationists who make much greater claims for that theory than does De Vries himself.
>
> Second. Each generation of biologists is so occupied with its own work and contemporary theories that it makes no real effort to understand preceding theories.
>
> This second tendency seems to me most marked in the attitude of present workers along genetic lines towards natural selection. They reveal an apparent lack of understanding of what Darwin really meant and of what he claimed: and when criticising that theory they are often engaged in the classic, but unprofitable, exercise of "fighting windmills."

Huxley (1948, reprinted from 1927) has reviewed the rise of selectionism and the fights against it among professional biologists.

> Many of them were ripe for conversion to the idea of evolution but before 1859 no one had put forward any but the most improbable suggestions as to how evolution could have been brought about. . . . This Darwinian view of evolution was generally accepted by biologists in the latter part of last century. But about 1890 doubts began to be thrown upon it, and around 1910 it had become so unfashionable that some critics proclaimed the death of Darwinism. By Darwinism, of course, was meant the selectionist theory of the method of evolution: the fact that evolution has occurred was never seriously questioned by biologists after 1859, except for a few survivors from the pre-Darwinian period, and a very few later cranks. . . . This sceptical attitude of the early twentieth century was due to two main causes. For one thing, orthodox Darwinism was tending to become purely speculative, invoking natural selection to explain anything and everything without requiring proof and without providing any explanation of the machinery by which the results could be brought about. . . . In the last twenty-five years, however, . . . the balance has now swung over heavily, and, I think, permanently, in favor of Darwinism or selectionism. . . . It turns out that the reports of the death of Darwinism, like those of the death of Mark Twain, were very much exaggerated. Indeed, the net result of the last quarter century's work in biology has been the reestablishment of natural selection as the essential method of evolution, and its reestablishment not merely where Darwin left it, but on a far more secure footing. For one thing the alternative explanations have ceased to be plausible.

Hofstadter (1945: 174 *et seq.*) presents an interesting interpretation of the early acceptance of Darwinism in America, particularly by non-scientists.

> . . . American society saw its own image in the tooth and claw version of natural selection. . . . As long as the dream of personal conquest and individual assertion motivated the middle class this philosophy seemed tenable, and its critics remained a minority.

Although, as Huxley observed, the theory of natural selection was quickly and widely adopted, sometimes in such extreme form as that advocated by Weismann, it was not accepted by all biologists nor were all the dissenters either cranks or intellectually out of date. Many were highly competent and profound scholars.

This same theme was given by Huxley in 1940 (p. 3) when he said that

> One of the most striking features of recent evolutionary theory has been the swing-back to a selectionist interpretation, after the anti-selectionist interlude initiated by Bateson, de Vries, and Morgan. It should be further emphasized that this has been most marked among those who have been in closest genetic contact with the problem. . . . We may safely prophesy that the anti-selectionist views of those not so directly concerned with the machinery of evolution, notably among the experimental biologists and the paleontologists, will be dissipated as the implications of modern genetics become more widely realized.

Huxley's statement that de Vries was anti-selectionist is not easily sustained, except in a special sense, by the writings of de Vries who frequently spoke of natural selection in such terms as the "principle which rules the evolution of organisms" (1912: 6), or as "the one directing cause of the broad lines of evolution" (p. 7). De Vries did of course contend (p. 825) that "Natural selection may explain the survival of the fittest, but it cannot explain the arrival of the

fittest." This belief that natural selection is merely a sieve has been expressed by a great many other writers, for example: J. M. Baldwin (1896); Cope (1887: 16), ". . . nothing ever originated by natural selection"; Darwin (1896); Henslow (1894: 264), "Therefore Natural Selection has nothing to do in aiding the Origin of Species"; Lotsy (1916: 135, 160), *"Crossing therefore is the cause of the origin of new types, . . . selection is the cause*—not of their origin . . . but *of their extinction*. . . . Selection is only 'une belle phrase' for extinction, the forms last exterminated, being called the selected ones"; Morgan (1905: 64–65), ". . . the theory of natural selection has nothing to do with the *origin* of species, but with the survival of already formed species"; Wallin (1927: 5), "Natural selection can only deal with that which has been formed; it has no creative powers."

J. T. Patterson (1942: 154) observed that Darwin's work "did not elucidate the *modus operandi* of species origin and differentiation" because it did not account for the origin of variations. Much earlier Cope (see 1887), a grossly neglected and misinterpreted author, had approvingly quoted a still earlier remark that "what the hypothesis of evolution wants is *a good theory of variation.*"

Further, as a matter of fact, paleontologists have not been so anti-selectionist in point of view as Huxley intimates although his comment has been repeated frequently, particularly by biologists who have not been thoroughly familiar with the nature and extent of the paleontological record and its more recent interpretation by paleontologists.

The good theory of variation, which Cope wanted, has of course been partly supplied by Mendelian genetics, a subject which has also directed attention to extremely small morphologic variations (if we choose to regard chromosomes and plasmagenes and their parts as morphologic materials), has eliminated or made implausible many speculations about selection which were previously tenable, and has strengthened the evidences for natural selection. According to Watson (1936: 45), "The theory of natural selection is the only explanation of the production of adaptations which is consonant with modern work on heredity. . . ." Castle (1917: 387) after observing the temporary obsolescence of "Darwinian selection," following the development of de Vries' mutation theory and Johannsen's pure line theory, stated

> I am not ready to say that natural selection is proved as the method *par excellence* of evolution, but I am not ready to abandon it as the most reasonable explanation of evolution until something better supported than the mutation theory is offered as a substitute for it. . . . Even though the mutation theory cannot be accepted as a general theory of evolution it has done us great good in dispelling or clarifying the hazy notion which formerly existed as to what natural selection could accomplish.

THE CREATIVENESS OF SELECTION

What natural selection can accomplish has continued to be the subject of numerous debates. Several members of the "survival but not arrival" or the non-creative school have been quoted above. Other authors have maintained that natural selection can be or is creative. Davis (1949: 67) reviews the more recent genetic point of view on the creativeness of natural selection: "Under the directive influence of selection, new genetic systems arise. . . . The creative role in evolution is thus assigned to selection." Holmes (1948*a*: 328) finds it ". . . impossible to maintain that natural selection [as he defines it] is a purely negative influence. Without variation it may not create a new species. Neither can variation without the preservative action of natural selection." Nutting (1921: 131) expressed the opinion of many other authors by saying,

> The statement has often been made that natural selection "originates nothing" because it does not explain the origin of variations. I must confess to scant patience with this point of view. As well say that the sculptor does not make the statue because he does not manufacture the marble or his chisel; or that the worker in mosaic originates nothing because he does not make the bits of stone which he assembles in his design!

Simpson (1947: 493–494) in discussing the new or synthetic theory of evolution says that natural selection ". . . on a new basis and in a new role, a process subtly but fundamentally different from the natural selection of Darwin or of the neo-Darwinians," is

> not merely the negative process of elimination of the unfit, by assuring that they will have fewer offspring than the fit: it is the positive and creative process that was left out of the picture by the Darwinians and was sought in vain by the Lamarckians, the vitalists, and others. . . . Clearly the critics of natural selection, in the old sense, were quite right in concluding that merely eliminating inadaptive combinations would rarely, if ever, insure the appearance of adaptive combinations. . . . But it has been

demonstrated both theoretically and experimentally that selection acts in a positive way tending to increase the percentage of favorable genes in a population. . . . It thus greatly increases the chances not only of favorable single genes but also favorable hereditary combinations.

In the new sense, although selection does not create the raw materials, mutations, it "is definitely creative. It creates the most important product of all, the integrated organism. Builders do not make bricks, but they create houses, and the bricks are not adapted to a use until they are assembled into houses."

Simpson's earlier statement (1944: 31), in a discussion of variability, that the action of natural selection on intergroup variation can produce nothing new, ". . . it is purely an eliminating, not an originating, force," was challenged by Wright (1945: 416) with the comments that

A single choice between two types may indeed appear eliminative rather than creative, but a succession of choices has a guiding influence that I think may properly be called creative irrespective of the level at which the choices are made. I would consider the drastic elimination of families and orders of vertebrates, and the compensatory adaptive radiation of the successful ones, as highly creative with respect to the major course of evolution.

THE ROLE OF SELECTION IN EVOLUTION

Between the extreme selectionists, such as Weismann and his satellites, and those to whom natural selection as a theory became untenable or ". . . an improbable assumption . . ." (Berg, 1926: 35), may be found the majority opinion of biologists and paleontologists who regard natural selection as one of the factors, but not the only factor, in progressive evolution. Among the more revealing works from differing points of view, the following may be indicated as expressing various ways that natural selection is an effective fraction of the evolutionary total: Ashley-Montagu (1947, cited above); Babcock (1944: 386), "But it is only one of several factors"; Blum (1935: 368), in considering evolution from a thermodynamic point of view, ". . . natural selection must have played an important part . . ."; Conklin (1912, and in many other works); Cope (1887: 16), ". . . natural selection, . . . is but half the question, and indeed the lesser half. It is to the great causative forces as are the gutters and channels which conduct the water in comparison with the pump and the man who pumps it"; Eimer (1898: 21), natural selection is at most a "collateral instrument" to orthogenesis; Haldane (1932*b*: 187), ". . . it would seem that the main burden of causing evolution must be thrown on natural selection . . ."; Metcalf (1913: 66), ". . . some of the advocates of natural selection have gone too far"; Wallin (1927, cited above); Watson (1929: 9), it is ". . . difficult to appeal to natural selection as the main or indeed an important factor" in evolution although it may be ". . . the principle which overrides all others . . ."; Willis (1940: vii), in a discussion of the assumptions of natural selection, concludes that natural selection's place ". . . is one of great importance . . ." but that it is not required as a support for evolution; Wright (1932: 359), "To evolve the species must not be under strict control of natural selection."

The difficulty of obtaining satisfactory evidences for the actual operation of natural selection even among living organisms has been frequently emphasized, and the nature and the acceptability of the evidence depend of course upon the meaning of natural selection and its relationship to evolution. Berg (1926: 66) observed that natural selection, or in the simplest sense, the survival of the fittest ". . . expresses a self-evident truth, for the fittest is the best adapted for life; and therefore the survival of the fittest means the survival of whosoever can survive." Similarly, Dewar referred to the "survival of the luckiest" and McAtee (1936) regarded the "selectionist idea of fitness" as "an impossible one" because in natural catastrophies and other cases survival is not related to fitness, and concluded that fitness "is distinctly a qualification that must be individually acquired, and . . . is not inherited nor can it be transmitted . . ." and thus "loses most of its importance for the theory of natural selection" (p. 240).

Differential survival among the members of a group may be an obvious fact but opinion divides again in a discussion about whether natural selection can "act upon" very small structural or adaptational differences and thus confer advantages upon the present living "selected" individuals or upon their future descendants. Little space can be given here to this very important aspect of natural selection and adaptation but a few of the more widely-held opinions are worth quoting because of their significance to the study of natural selection in paleontology and to the taxonomic aspects of paleozoology.

Cope (1887: 15) reasoned that natural selection fails to account for the structures of many

organisms because the survival of the fittest ". . . requires that the structures preserved should be especially useful to their possessors . . ." whereas many of ". . . the peculiarities of the parts of animals (and probably of plants) are of no use to their possessors, or not more useful to them than many other existing structures would have been."

Bailey (1941) discounted the effectiveness of natural selection in the direct preservation of small morphological variations, and stated his belief (pp. 228, 229) that

> . . . in many organisms physiological variation is more pronounced than morphological variation. And even in those cases where considerable morphological variation occurs the elimination of unfit individuals by the action of natural selection may prove in the final analysis to be physiological.

Beecher (1901) mentioned several obscure "causes" for the origin of spines in his thesis that natural selection ". . . could not originate a spine . . ." but could preserve it and allow it ". . . to develop along certain lines" after it had appeared. In discussing the question, "Does natural selection play any part in the origin of species among plants?" Henslow (1897) answered in the negative because no "vital importance" can be attributed to "trivial" morphologic distinctions.

In 1906 V. L. Kellogg (p. 627) announced, after some studies of the California flower beetle, that he was

> . . . done with meekly accepting the dictum of the selection champions who declare . . . that we do not know what difference . . . a very slight modification of pattern may produce; that we can not say of any difference, however minute, . . . that it is not the hair in the balance; and that when we understand *all* the conditions of life of an organism, then, and only then, are we entitled to say of this or that character that it is not of life-and-death value.

He concluded, logically, that the changes he thought he had observed were not due to natural selection.

Metcalf (1928), Sumner (1929), and Schaffner (1937 and elsewhere) have discussed the difficulty of believing or demonstrating that the incipient stages of characters can be subject to selection. Metcalf and Schaffner were led to credence in orthogenesis and other alternatives, and Sumner concluded that the truth, ". . . as now generally accepted, is intermediate between the extreme positions . . ." which he reviewed.

In controverting the opinion that small differences are not influenced by selection, several authors have recently published statistical and other evidences for believing that very small structural and physiological fluctuations are subject to selection, that it is not necessary for the effects of selection to be of ". . . obvious life or death value to be effective" (Wright, 1939: 53), and that selection of "small physiological" mutations actually does occur (Timoféeff-Ressovsky, 1936: 46–47). Fisher, although he has commented that "Natural Selection is not Evolution" (1930: VII), has also pointed out that

> . . . when the matter is viewed . . . in relation to the calculable magnitudes of the selective agencies at work, and to the known effects of selection in artificial cultures, it is clear . . . even with the extremely minute selections favoring recessiveness in the mutants of *Drosophila*, that they are quantitatively of a magnitude sufficient to have produced the effects ascribed to them . . . [1931: 367].

According to Mather (1943: 33) in commenting upon the work of Fisher and others, "Natural selection is a phenomenon separable from evolution and capable of being studied independently," and he also develops the concept, of great significance to taxonomy and paleontology and to general evolutionary studies, that variability ". . . may be hidden in the genotype under the cloak of phenotypic constancy . . ." (p. 62) and thus be removed from the direct influence of selection. Muller (1929: 488) had previously written that

> Evidence is not lacking that physiological changes, and changes that can only be detected physiochemically, are probably as frequent as changes in visible structures, but geneticists have till now had to have a predominantly morphological training, and anyhow the morphological is easier to see and deal with. It would be absurd and scholastic to try to classify mutations according to the nature of their effects.

SELECTION AND MUTATION

As soon as variability of the phenotype was traced to the condition of the genotype it became necessary to determine the relationship of natural selection to genetic materials and to try to answer the question "Can natural selection cause or lead to mutation or other genetic change?" Negative answers, such as those of J. T. Gulick (1908), from his studies of snails, and Pearl (1917) from his own research and a review of the work of other authors are common in the literature on the subject. Castle (1916, 1917) had taken

issue with Pearl but concluded that many of their differences were ". . . verbal rather than real." Later, Muller (1929: 488) replied to his own question "Do variations have a tendency to be adaptive, to further life?" by saying that ". . . the data on the actual occurrence of mutations show just the opposite. . . . The vast majority of observed mutations are positively detrimental. . . ."

Many other authors have stressed the apparent fact that most known mutations and other genetic changes, or, in earlier writings, spontaneous variations, are not adaptive. Some of the most pertinent and varied statements of this conclusion are to be found in Berg (1926: 33); Caullery (1933), who even finds every appearance of real morphological adaptation to be delusive (p. 7); Colin (1941: 335 *et seq.*); Cope (1887); Cowles (1946: 74); Darwin (1896); Davenport (1916: 460); Dobzhansky and Spassky (1947); Hurst (1932, 1932*a*); Huxley (1944); Muller (1929, 1947); Sturtevant (1937); and Wright (1939).

As always, however, there are dissenting opinions. East (1936: 155) suggests that ". . . constructive mutations are numerous but have ordinarily remained unnoticed . . . ," and Hooton (1931: 598 *et seq.*) found the orthodox notion of natural selection operating on chance variations ". . . a depressing business . . . that necessitates an inconceivable credulity on the part of its believers" (p. 600).

Whether the kinds of mutations studied by geneticists and whether the known rates of mutation are adequate to account for the broad historical sweeps of evolution are very important questions in paleontology. Again opinion divides. Babcock (1918: 127) believed it probable that

> . . . factor mutations alone have furnished the necessary germinal changes to make possible the evolution of the elephant's trunk and similar cases of orthogenetic development which have been discovered by paleontologists. But factor mutations alone are not sufficient . . . to account for . . . the appearance of phyla and genera.

Coe (1924: 147) pointed out that the "most profound" known mutations have produced only new breeds or varieties: ". . . no unquestionable new species have been created under human observation. Do species also originate from mutations . . .?" A. H. Clark (1930), in developing his theory of zoogenesis also asked how, from the study of the "relatively slight" mutations of laboratory and field breeders, it is possible to assume that mutation could account for the differences between higher categories. Clausen *et al.* (1939: 103) observed that "Very few cytologists or geneticists study their plants or animals except in the laboratory, and the forms studied are seldom representative of those found in any natural environment."

Griggs, ardent supporter of orthogenesis, thought that "You might as well argue about the random aberrations of a canal boat swinging on its tow-rope as compared with the course of a ship on the open sea, as to conclude that the random mutations of *Drosophila* tell us much about the evolution of insects" (1939: 135). Conversely, a few years later J. T. Patterson (1942) reported that, from studies of *Drosophila*, "It is no longer necessary to explain evolution by analogy, for the application of genetical and cytological techniques in this genus proves that it depends on experimentally measurable gene mutations." MacBride (1938), in support of a Lamarckian interpretation, regarded "artificial mutations" in the laboratory as ". . . no proof whatever that mutations have had anything to do with the formation of species." From a quite different point of view Fisher (1936: 59) also found that "The explanatory content of a theory of evolution only reaches its absolute zero with the mutation theory."

Schaffner, who so firmly and vigorously and naively rejected natural selection, often (e.g., 1932: 337) expressed the same or a similar theme: the mutations of the experimentalists ". . . are not of the category one encounters in the study of the evolution of organisms." Other authors (e.g., Sturtevant, 1937; Timoféeff-Ressovsky, 1940) have thought that mutations of known kinds are the only or almost the sole, source of new or raw evolutionary materials. Many geneticists, however, Haldane (1932*b*: 188) and Wright (1932, 1939: 5–6) among them, have pointed out that genetics does not furnish a complete basis for a theory of evolution. Further, the knowledge that not all heredity is through mendelizing genes has been recently stressed in different ways by Little (1947) and Sonneborn (1949). Nevertheless, changes in chromosomal genes and plasmagenes are regarded as the basis for all evolutionary differentiation. As Muller expressed it in 1926 (p. 913),

> It may be reiterated at this point that there is no good evidence from genetics of any heritable differences between organisms except such as are resident either in the numerous genes of the nuclear "chromatin," or, much more rarely, in the plastid primordia, which

may contain a homologous substance. And since our evidence is extensive, and the phenomena of heritability a highly peculiar one, it is logical to conclude that in all probability all specific, generic, and phyletic differences, of every order, between the highest and the lowest organisms, the most diverse metaphyta and metazoa, are ultimately referable to changes in these genes—chiefly in the multitudinous and very diverse chromosomal genes, to a lesser extent in the plastid genes.

From this point of view some knowledge of the gene and the plasmagene belong in the research kit of the paleontologist.

SELECTION AND GENETICS IN PALEONTOLOGY

If genetics concepts have been slow to permeate other scientific disciplines, particularly paleontology and anthropology (as several geneticists have observed), the reason may be found, in part at least, in the lack of definition of some genetic concepts, in the absence of unanimity of opinion among geneticists, in the speed with which novelties in genetics experiments and conclusions are developed, and in the natural development of a special and esoteric jargon in genetics. The notion that a one-to-one relationship existed between gene and single morphological structure or character is old and for a time appealed, in its simplicity, even to geneticists. Hagedoorn and Hagedoorn (1921: 44 *et seq.*) discussed the ". . . naive idea, that every character or every organ has its own 'determinant' . . ." and the consequences of the idea, and A. L. Hagedoorn as late as 1932 reported that the old conception of genes ". . . as living protoplasmic corpuscles, each kind determining some definite character or part . . . even today seems acceptable to the majority of geneticists." In view of genetical conclusions such as those expressed by Haldane (1932, 1937) and by Stern (1949) regarding the relationship of gene and character, comments similar to the following do seem to be anachronistic or at least to be open to misinterpretation: "It is separate traits, and not aggregations of traits, which must be studied [in anthropology], for the simple reason that it is the former and not the latter which are inherited . . ." (Ashley-Montagu, 1947: 121).

Paleontologists have long hoped that geneticists would answer definitively the question "Do observed natural mutation rates, regardless of their cause, accord with the known fossil record?" The answers must be given, of course, in terms of current estimates of geological time. In 1889, when Hyatt wrote that Neumayr's view, of exceptional speed of modification among the cephalopods, seemed erroneous, all of geological time was generally estimated to be less than a tenth as long as the most recent calculations suggest (see Knopf, 1949). De Vries' conclusions about the necessity for rapid changes, for mutations of profound effect, were undoubtedly influenced by the estimates his contemporaries made of geological time.

To Evans (1949: 302, 304), "It is interesting to note that cosmic radiation and local gamma radiation . . . are entirely inadequate to account for the natural spontaneous gene mutation rate . . ." which "is therefore due to other causes than irradiation." Haldane (1949*a*: 56) finds that "The observed rates of mutation are quite large enough to account for evolutionary changes," and Wright (1945: 416), in discussing Simpson's (1944) extensive observations upon evolutionary rates, states that

> The situation is such that under exceptionally favorable conditions great evolutionary advance is possible at an explosively rapid rate. It should, of course, be added that while mutation rate is probably not a limiting factor, new alleles may actually be expected to appear following radical changes in gene frequency.

The scales of morphology and of time to geneticists are so different from those of paleontologists that the comparative terms of "fast" or "slow" have very different meanings about the rate of evolutionary change.

Other semantic and factual difficulties in discussing natural selection from the paleontological viewpoint arise from differences in the meaning of the word "species," as noted above. They will continue to plague the paleontologist, despite the remarkable statement of Arkell and Moy-Thomas (1940: 396) that "The question 'What constitutes a species?' always so troublesome to neontologist, hardly concerns the paleontologist . . . ," as long as natural selection is discussed in terms of species, as it customarily is.

Although the whole subject of species and speciation is germane to the present topic, it is impossible herein to select a path through the extensive literatures about varieties as incipient species, the kinds and degrees of isolation necessary for different rates and kinds of speciation, and the many notions about slow *versus* rapid multiplication of species. It is worth pointing out, however, that some of the recent discussions

about species are more concerned with standardization than with nature. If only for the sake of exchanging ideas there must be several concepts of species to describe the many natural situations which are being studied. As Mayr (1948: 208), says, species are products of nature and not specially made for the convenience of anyone. Nevertheless species *concepts* are artifacts, and the recent return to some of the oldest concepts of species, based upon breeding and sterility situations or upon genetic discontinuity, is no advance for paleontologists and other anatomists.

Allowances must be made for differences in point of view. To the paleontologist, accustomed to seeing the minute morphological fluctuations in a population of one species slowly change, as the group rises through geological time to become a different species (in terms of any definition), the one certain fact about the two species is that they are genetically connected.

Two final questions may be asked in these comments about natural selection: How is it defined in current thought? What evidences does paleontology provide in connection with it?

Nash (1944: 542) defines it as ". . . the perpetuation of the fittest to perpetuate, which connotes the perpetuation of genetic factors that increase fitness for reproduction as well as of those that increase fitness for personal survival." To Haldane (1936: 67) "Natural selection may be defined as the elimination from a genetically mixed population of the less fit genotype." Holmes (1948*a*) says that natural selection ". . . is a name for a group of processes that make for the preservation of an organism or its destruction as a result of its inherited constitution" (p. 326), and that he includes in the term natural selection ". . . the multitudinous phenomena of development, the physiological activities of all parts of the organism, its behavior in relation to external objects and conditions, and the effects of the environment on the life of the individual" (p. 328).

It is virtually impossible to demonstrate "that natural selection has altered a race," if the "basic and minimal logical requisites" for such demonstration, as outlined by Pearl (1930) are really necessary. He demands proof of somatic and genetic differences between survivors and eliminated, of effective time of elimination, and of somatic and genetic alteration of race. Paleontology offers no such positive proofs, nor for that matter is it likely that neontology can at present provide any satisfactory examples.

The very nature of fossils makes their evidence for vital processes indirect. This is not necessarily a deficiency, however, nor is it confined to the study of fossils. Paleontology supplies circumstantial evidence for many phylogenetic and environmental events, and for all known long-term sequences of genetic effects. In spite of the inadequacies of the record there are now probably more good studies on the skeletal anatomy and also on the external morphology of the brains (see Edinger, 1949: 6) of fossils than of living animals.

Natural selection, as studied in living or in fossil forms, is presumably to be tested by the ways that species develop fitness or adaptation to the conditions of life. To some authors organisms are bundles of adaptations; to others adaptation is nonsense. The subject offers exceptionally wide fields for controversy, as mentioned above, and for speculation and imagination.

In general, adaptations are, to the paleontologist, the correlations, useful to organisms, between environment and structure or ontogeny, and are usually expressable in terms of function. As Watson points out (1929: 3), some function-morphology correlations such as the structure of an ichthyosaur and an aquatic environment are obvious but that some, such as the postcranial skeleton of a hippopotamus and water dwelling, are not.

Adaptation in phylogeny has frequently been treated as a simple one-to-one correspondence of structural and environmental factors, but this simplicity is not tenable in the light of several genetic concepts such as pleiotropic genes and multiple-gene and rate-gene effects.

Speculations about adaptation, and, through this channel, about natural selection, are deceptively easy to make. The giraffe's long neck as an adaptation for high eating has been cited as an example both for and against natural selection, but no one, so far as I know, has suggested that the primary adaptive function of the length of the creature's neck has little or no connection with the ability to secure food. There are, however, alternative possibilities that may merit future consideration.

If it is possible to question the basic function of some of the structures in the most hackneyed examples of natural selection and adaptation among living animals, it must be downright foolhardy to attribute function to long extinct structures or to attempt to perceive the operation of natural selection in the remote past, even by

analogy, and yet perhaps it is worth while to try to do so.

MULTITUBERCULATES AND RODENTS AND SELECTION

One process or consequence of natural selection which may be perceived with varying degrees of reliability in the fossil record is the replacement, in a certain ecologic niche and locality, of one group of organisms by another unrelated but morphologically similar group. Several kinds of such succession in nature's economy have been described: (1) the earlier or older group may have been extinct long before its place becomes occupied by the later group, (2) the replacement may occur immediately after a niche is vacated, either through very rapid evolution or through changes in ecologic preference of another group, or (3) the decline of one group may be coincident with and influenced by the expansion of its ecologic successor.

Although many examples of the first two kinds of replacement are in the literature on fossils, examples of the third kind are less numerous. All three have sometimes been cited as either convergence or parallelism although each of these two terms has also been applied to several different phenomena.

Many millions of years intervened between the disappearance of the Mesozoic marine ichthyosaurian reptiles and the appearance of their mammalian morphologic and ecologic analogues, the Late Tertiary and Recent porpoises and dolphins and other small whales.

A case wherein the extinction of an earlier group may have provided a habitat which another group could occupy immediately thereafter, the replacement of the phytosaurs by the crocodilians in the Mesozoic, is described by Colbert (1949*a*: 402):

> In Late Triassic times, when the phytosaurs were at the height of their dominance as aquatic predators, the first crocodilians were making their appearance as small upland-living reptiles. While the phytosaurs were dominant these ancestral crocodilians were limited by selection pressures to their initial upland mode of life, a mode of life not greatly different from that earlier enjoyed by the ancestors of the phytosaurs. But with the extinction of the phytosaurs a new habitat was opened to the primitive crocodiles, and within a remarkably short duration of geologic time these reptiles shifted from one environment to another, just as the phytosaurs had done at the beginning of the Triassic period, to become during Early Jurassic times fully adapted aquatic predators, fulfilling in every way the same ecologic role that had been fulfilled during the Triassic period by the phytosaurs.

As an apparent example of coincident decline of one group and expansion of another in causal relationship the geological record of the multituberculates and the rodents may be cited. Multituberculates are usually classified as mammals, but their position in mammalian taxonomy and phylogeny is questionable. Their unique structures of skeleton and teeth have permitted the speculation that they may have been derived from reptiles as a stock separate from all other mammals, or that, physiologically they may never have become mammals. In general appearance or in habitus, and probably in food preferences and other habits, they were rodent-like. Thus, the multituberculates may be called the economic, but not the phylogenetic, ancestors of the rodents.

Multituberculates were very successful for a very long time. Their known history ranges from Late Jurassic to Early Eocene, a period of approximately seventy-five million years. Only two other orders of mammals, the marsupials and the insectivores, with a phylogeny beginning in the Late Cretaceous, have equally long histories. This durability of the Multituberculata and the fact that the order contains more genera than most orders of living mammals suggest a high degree of adaptation and adaptive plasticity. Only three of the fourteen orders of extinct mammals contain more genera than the Multituberculata.

From Late Cretaceous to Early Eocene times, during the last fifteen or twenty million years of multituberculate existence, a small ptilodontine form (*Ectypodus, Ptilodus,* etc.) persisted almost unchanged. The rate of change was so slow that it must be reckoned in millidarwins or in even smaller units than any proposed by Haldane (1949*a*). The skulls of this type are between one and two inches long; the living animals were about the sizes of rats and mice. Although their cheek teeth are not similar to those of rodents, the single incision in each lower jaw of the ptilodontines superficially (in shape and attitude and position) resembles the corresponding chisel-like tooth of a rodent. In surface detail and microscopic structure, however, there are significant differences between multituberculate and rodent incisors (Jepsen, 1937, 1940). The latter grow from persistent pulps and the wear at the tip is compensated by continuous growth at the end of the root and a consequent gradual extrusion of

the whole tooth, whereas ptilodontine incisors had closed roots and lacked a mechanism for replacing the tip when it was worn away.

Although the whole tip of an unworn ptilodontine incisor was covered by enamel, in rodents the enamel occurs only as a band along the front edge. Thus, in rodents, the differential hardness of enamel and dentine provides a self-sharpening chisel. Once the enameled tip of the ptilodontine incisor was removed, however, the tooth was a comparatively poor eating tool. Multituberculates apparently had but a single set of teeth. No specimen among the many known shows the characteristic eutherian replacement of milk teeth by a permanent set.

These differences between the teeth of multituberculates and rodents may have been a major factor in the gradual disappearance of the former during the spectacular rise of the latter.

Table 1 indicates the known Tertiary record of the numbers of genera and species of American multituberculates. They were abundant during the Paleocene not only as generic and specific groups but as individuals as well. The number of genera steadily increased in this time whereas the number of species first increased and then decreased—a pattern which, if it reflects actual history, has several interesting possibilities of interpretation.

From rocks of Early Eocene age only a few specimens of multituberculates are known—they are extremely rare. Further, when Early Eocene time is subdivided into earlier (A) and later (B) parts, it is possible to express the even more precise record of the extinction of multituberculates *during* Early Eocene time. Representatives of three genera and five species have been recovered from the lower strata, but none have yet been found in the upper rocks, of Early Eocene age. It is particularly significant that this record has been principally compiled from a relatively small area, the Bighorn Basin and the surrounding region in Wyoming and southern Montana, and that there are no known breaks or gaps in the sequence of sedimentary events.

Rocks in the same region (from Early Paleocene to Early Eocene age, inclusive) have yielded the earliest records of the rodents, the group often called the most successful living order of mammals, believed to be as numerous, as individuals and as kinds, as all other mammals together.

The earliest known rodent is of Late Paleocene age (Jepsen, 1937), and its occurrence is coincident with a marked decrease in the number of species of multituberculates. Rodent species and individuals increase in number in Early Eocene A, expand greatly in B, and then undergo what is sometimes called an evolutionary explosion—an explosion which has continued for more than fifty million years.

TABLE 1

NUMBERS OF GENERA AND SPECIES OF EARLY TERTIARY MULTITUBERCULATES AND RODENTS

Epochs		Multituberculates		Rodents	
		Genera	Species	Genera	Species
Eocene	Late	0	0	13	31
	Mid	0	0	9	19
	Early B	0	0	3	8
	Early A	3	5	1	4
Paleocene	Late	7	11	1	1
	Mid	6	17	0	0
	Early	5	7	0	0

However, the early record of apparent ecological replacement of multituberculates by rodents is even more striking. It is in fact almost too perfect. About a dozen small areas in America have yielded large collections of Paleocene mammals. In all these sites except one multituberculates are among the commoner kinds of fossils. The exceptional locality, at Bear Creek, Montana, is the only one where rodents occur. This absence of multituberculates and presence of rodents was so unexpected that some of the rodent teeth from this site were at first attributed to multituberculates.

This speculation that the expansion of rodents was principally responsible for the decline and disappearance of multituberculates does not, of course, explain the origin of rodents nor does it answer the many other questions that come to mind. Neither is there any irrefutable evidence that the differences in incisor structure were a major factor in the events as they are interpreted, but these suggestions are compatible with the concept of natural selection and do not necessitate appeal to racial old age or to orthogenesis or any other non-selectionist interpretation to help explain the apparent historical circumstances.

ORTHOGENESIS AND ITS ADVOCATES

Orthogenesis (literally "straight origin") as a biological term was apparently first used by Haacke in 1893 and was soon appropriated and redefined and popularized by Eimer (1898 and

elsewhere) to mean "definitely directed evolution" which was caused "by external circumstances and influences such as climate and nutrition upon the constitution of a given organism." It might be either adaptive or inadaptive and was a "universally valid law." This was a continuation of what Eimer had earlier (1890) proposed as a theory of evolution "governed by definite laws," and was intended largely to replace Darwinism and "Weismannism." Eimer, in a series of vicious attacks upon Weismann, asserted that transmutation rests upon the inheritance of acquired characters although he emphatically rejected Nägeli's internal perfecting principle, and he argued that the whole transformation of organisms was a physiological process conforming to physico-chemical laws. Natural selection at best could merely preserve existing species (see above) and was entirely subordinate to orthogenesis. Eimer framed several specific biological laws, a strong predilection of his time, and noted with approval that the work of the Americans, Hyatt (on ammonites) and Cope (on fossil vertebrates), seemed to confirm some of these laws.

Soon, of course, "orthogenesis" was being used for many different concepts, as Simpson (in press) and Plate (1913) among others, have recorded. Many recent authors, however, apparently assume that "orthogenesis" has always meant straight-line evolution controlled only by innate constitution, or by extra-mundane factors, and not by environment.

It is also commonly and erroneously assumed, particularly by biologists and anthropologists, that orthogenesis was not only conceived and developed and demonstrated by paleontologists but is still held in high esteem by them, and that the main "evidences" for orthogenesis or similar theories are to be found in studies of fossils. Paleontologists or paleontological facts are thus alleged to furnish evidences along the lines of orthogenesis by the following authors: Ariens Kappers (1942), Berg (1926), W. E. LeGros Clark (1934), Coe (1924), Crile (1933), Davenport (1916), Griggs (1939), Haldane (1932*a*), Holmes (1948*a*), Howells (1944), Hurst (1932), Huxley (1940, 1942, 1944), Jeannel (1942), V. L. Kellogg (1908), Mayr (1942), Metcalf (1928), Newman (1921: 36), Rensch (1938, 1947), Schaffner (e.g., 1937), Shull (1935), Sturtevant (1924), Sumner (1929), Wheeler (1947), and Wright (1939).

In a current (and not yet complete) survey of the literature, however, it has become apparent that orthogenesis has been accepted *as a theory* more by biologists and, recently, by biochemists than by paleontologists, and perhaps more by paleontologists than by biologists *as a descriptive term* for phylogenetic arrays. It is notable and perhaps remarkable, that Shull, a biologist, wrote in 1935 that "What the world most needs, then, is not a good five-cent cigar, but a workable—and correct—theory of orthogenesis."

Neontologists have frequently arranged their materials in graded fashion and have then appealed to orthogenesis to account for the fact that such arrangements are possible. Some arrays are based upon minute differences in the color patterns on insect wings or on the bodies of lizards, and others upon much more profound variations among contemporary forms, but the assumption is usually made that the range of diversity from the smallest to the largest magnitude, or between the extremes of pattern or structure, is the result of orthogenesis. Frequently one end of the layout is selected as the more primitive and is hence said to be a relict survivor or a "structural ancestor" which is unchanged from the ancestral form that gave rise to the next form in the array, and so on, as a series of step-projections from the past to the present. Eimer based his conclusions almost entirely upon living forms and other authors have done the same, either in support of orthogenesis or to discredit it: Boulenger (1907), siluroid fishes; Caullery (1931), *Gammarus;* Coulter (1915), gymnosperms; Crile (1933), man; Dean, (1904, 1912), egg capsules of chimaeroid fishes; Eyster (1926), "orthogenetic series of genetic variations"; Gadow (1899), turtles (but see Grant, 1937, for criticism), (1904), lizards; Gislen (1934), echinoderms; Griggs (1939), several examples; Guyer (1922) "in serological phenomena"; V. L. Kellogg (1906), beetles; Kofoid and Swezy (1921), unarmored dinoflagellates; Linden (1897), molluscs; Ruthven (1909), garter snakes (but see Guyer, 1922, for comments); Schaffner (1928, 1928*a*, 1929, 1929*a*, 1930, 1931, 1932, 1936, 1937, 1939, 1939*a*, etc.), living plants and other organisms; and Whitman (1919), pigeons (but see Guyer, 1922). Fenton (1931) cites several other examples.

Several weaknesses in these graded arrays as examples of orthogenesis are obvious and have been remarked upon. Coe (1924: 129) suggested that ". . . most instances which have been thought to indicate orthogenesis are merely the result of a number of independent mutations from

an ancestral stock which the observer himself has arranged in such a series as to suit his theory." He mentioned paleontological series as falling in this category but his illustrations are of minute differences between living forms. Raymond (1939) however, in writing about lineages of greater magnitude, also stated that ". . . an orthogenetic line is one that is man-picked" (p. 306).

Boulenger (1907: 1062), observed that "It is sometimes the case that an orthogenetic series is susceptible of being interpreted in a reversed direction," but he thought that this was impossible in the group of living catfishes which he had arranged in "orthogenetic series." The sequence of somewhat similar groups was questioned by Guyer (1922), and Jacot (1932), in criticizing a monograph wherein orthogenesis within genera was discussed, said that "In a similar way I may arrange all the different types of bottles found in a Chinese junk shop in orthogenetic series—basing the series on size, degree of coloration, [and] surface sculpture. . . ." Lang (1938: 149–150) questioned the validity of arranging the "terms of a phylogeny" in an *a-b-c* direction instead of the opposite, *c-b-a,* direction when the "terms of a phylogeny . . . occur at the same stratigraphic horizon."

Introductory biology books almost without exception place the living egg-laying monotremes as the ancestors of the marsupials although there is not a shred of firm phylogenetic evidence from fossils for this arrangement. In fact Gregory (1947), in his interesting "palimpsest" theory, regards the monotremes as an off-shoot from the marsupials in the Tertiary, and not as persistent but somewhat modified Late Paleozoic or Early Mesozoic survivors.

Other reversals have occurred of what were long regarded as established and reasonable and logical probabilities supported by comparative anatomy and, to a lesser degree, by paleontology. The notions that cartilage is phylogenetically older than bone and that gills preceded lungs have become considerably less than probable, and the reverse order may be true in each case. Lam (1936) and Leach (1944) discuss similar popular misconceptions and reversals.

Now, with our mid-century advantage of retrospect it is possible to suggest evidences and motives for the historical development and vogue of orthogenesis, particularly around the turn of the century. The theory, as philosophers have reported, was in a way a recrudescence of the medieval notion that every occurrence could be correlated with antecedents in a perfectly definite way.

Orthogenesis, it is important to note, became a theory before our enormous collections of fossils had become accumulated, before the resurrection and expansion of mendelian genetics, and before the great development of biochemistry. At the present time more extinct than living forms are known in many groups of organisms, and genetics and biochemistry now furnish reasonable theories for more or less channelized and irreversible evolution. It is nevertheless pertinent to review some factors which contributed to the first and to some of the later bursts of enthusiasm for orthogenesis.

Orthogenesis was frequently expressed as a "law" at a time when there was an eager search for biological phenomena or principles which could be called laws, after the model of the eponymic laws of physics and chemistry. Some of the more interesting and entertaining discussions about the framing or perception or logic of biological laws are in the following: Berg (1926), Bradley (1938), Dendy (1915), Eimer (1890), Gregory (1935), Holmes (1948), Hyatt (1889, 1894), Noltenius (1936), Osborn (1912), Rensch (1938), Schaffner (1928 etc.), Scott (1894), Wheeler (1947), and Williams (1898).

At that time also, Haeckel's theory of ontogenetic recapitulation of phylogeny was in favor. By analogy, if the individual could develop in a straight line, as it obviously did in many ways, so could the race. Evolution was then visualized as being built of a few individuals in narrow lines of descent rather than of whole sequences of fluctuating populations. It was also built upon end products—adults—rather than upon genes and chromosomes and ontogenies. The rise and fall of "recapitulation" in popularity has received much attention in the literature and is especially interestingly presented in terms of its connection with orthogenesis and (or) its logical consequence, neoteny, by Ariens Kappers (1942), Berg (1926), de Beer (1940), Schindewolf (1936), Strømer (1941), and Swinnerton (1938).

A rigid faith in the complete irreversibility of evolution also helped some naturalists to accept straight-line single-direction proposals. Colbert (1949) discusses Dollo's concept of irreversibility and remarks that ". . . the course of evolution is *irrevocable* but the *direction* of evolution may be and frequently is reversible" (p. 119), and Gregory (1935, 1936) also has written upon the

meaning and limits of irreversibility and finds that uncritical extension of it has contributed, indirectly, to obscuring "the grand fact of transformation" (1936: 528).

The whole topic of reversibility is far too large for a review of its literature here, but some of the recent explanations, observations, and discussions of the degree of reversibility may be mentioned for their significance to paleontological interpretations. Blum (1935) in his aim of indicating the actual existence of a directing factor in evolutionary processes says that the principle of irreversibility has been shown to be required for the evolutionary process and that the direction of development is ". . . such as would be accompanied by an increase of entropy, the return over the same pathway being prohibited by the fact that it would involve a decrease in entropy" (p. 357). Florkin (1949) finds many examples of irreversibility of biochemical evolution and concludes that "Adaptation to a new environment will result in a modification of the arrangement of biochemical constituents to produce a new form of spatial hierarchy and to develop a new system or a new organ but not in the reappearance of an old one" (p. 129). He also speaks of evolution as a "regressive biochemical orthogenesis."

Timoféeff-Ressovsky concluded (1932) that some mutational processes are reversible, and Muller reported in 1939 that most mutations in *Drosophila* ". . . are reversible in direction, and very commonly the 'reverse mutation' appears to reconstitute precisely the original gene" (p. 276) but that despite these elementary steps ". . . reverse evolution as such cannot occur because of (1) the multiplicity of mutations and (2) the fact that a real identity of selective influences is precluded by the complexity of the circumstances which condition the selection" (p. 280). Chromosomal effects of radiation, however, are claimed to be irreversible by Mazia (1948).

To Romer (1949: 109–110) the phrase "irreversibility of evolution" is imposing

> . . . but is obviously absurd in broad interpretation and contradictory if stated in terms of organs. It is today difficult to understand how any great degree of adherence to this "doctrine" came about. Adherence to this creed has made it difficult to develop reasonable phylogenies for various groups for which there is an abundance of fossil material, and it has been responsible in many cases for the supposition that successive representatives of a group have not descended one from another, but that known types are a series of side branches from an unknown main line of "unspecialized" forms. . . . But evolution is definitely known to be reversible. Recent forms alone give strong evidence to that effect, and the paleontological evidence is conclusive.

Although the general idea that the numbers of possible adaptational changes is limited, or that evolution is not random in some senses, and hence has an orthogenetic cast (but without mysterious drives or forces), is old, it has been recently emphasized particularly by biochemists and geneticists, in significant ways. E. Baldwin (1937) says that the number of adaptational changes ". . . is sharply limited by the nature of the fundamental ground-plan, which therefore constitutes a limitation for evolutionary changes. . . ." According to Ford (1938: 48), as any evolving line ". . . becomes more highly specialized, the variations which could possibly be of use to it are progressively restricted. Finally, it attains a state of 'orthogenesis,' in which the only changes open to the species are those which push it along the path it has already pursued." In a discussion of "What are the genes?" A. Gulick (1938: 14) derives the conclusion that "The *directions* of possible mutations are not perfectly *ad libitum* but are limited to changes in such directions as can find expression in the gene complex actually in hand," and Haldane (1932*a*: 20) says "The gradual acceleration or retardation of a number of genes will lead to orthogenetic evolution."

In the 1922 symposium on orthogenesis before the American Society of Zoologists Henderson found it ". . . reasonable to suppose that apparent instances of orthogenesis may sometimes depend upon a single important chemical change in an organism, followed by slow progressive modifications leading up to a definitive morphological result" (p. 104). Muller (1949: 428–429) writes that

> Since any given [living] species has hundreds of millions of years of natural selection behind it already, it tends to have attained optimal degrees of development of its characters in relation to one another and to the conditions of life under which it lived. And any recurrent mutation having the frequency of origination dealt with in most genetic data would already have become selected and established in that species had it been advantageous under the conditions for which that species had been selected. If, however, the outward conditions themselves (under which we include of course the biological environment, constituted of other species) undergo some sort of shift, then some mutations formerly disadvantageous become advantageous and we may expect our given species gradually to change *pari*

passu, giving the appearance of orthogenesis. Even if the outer change be a relatively sudden one, the change in the given species may lag far behind, again proceeding gradually through an orthogenetic-seeming process. This is because all parts and characters of the organism are so nicely intercoordinated that a major change in one character, even though considered separately it might represent a better adjustment to the new outer environment, causes trouble until many other characters can be brought into harmony with it. Hence a small step in the character in question is for a time more advantageous, and then has to be followed up by small changes in the other characters before a further step in the same direction can be established.

B. Patterson (1949: 261) speaks of the genotype being "limited in its potential phenotypic expression" in such a way as to make certain effects "almost probable," and Wright (1939: 51, 53) observes that ". . . genes may mutate more easily to certain alleles than to others," and that "In many of the cases described as orthogenetic nothing more seems to be involved than adaptive advance along the only line open to a form which has, so to speak, irrevocably committed itself by specialized adaptations."

Other authors have also found ways that effective variation is non-random and have thus helped define a certain degree of channelized evolution. They have also removed some of the intellectual distaste which earlier workers discovered in the "completely random" Darwinian variation—a distaste which provided orthogenesis with a measure of popularity merely as a rebound from Darwinism.

Orthogenesis as a "law" and as the effect of innate internal or external forces can be and has been made to seem quite reasonable and logical and to express lack of information in such a way that further inquiry seems unnecessary and futile.

As Jennings remarks (1917: 298), "Looking back over the series from a later age, we are bound of course to find it a continuous development." But if we look forward can we predict the directions of evolution? Doing so is a favorite pastime of popular writers but the results are of dubious validity. Davies (1937: 173–174) in reference to the somewhat similar question "Where are the living species today that mark the beginning of new families, orders, classes?" was reminded of the pessimist who read an annual list of obituaries and then asked "What is the world coming to? Here are all these great men dead during the year and not a single great man born!" According to Edinger (1948: 33) "The brain connects *Eohippus* only with the past. . . . No feature of this brain signals the future," and Haldane (1949: 413) speculates that "If a Martian zoologist who knew no more than we do now about evolution had been asked to pick the most progressive vertebrate at any time in the past, I think he would very rarely have picked on the line which was destined to give rise to man." In short, "orthogenesis" is directional only when the direction is known.

Orthogenesis, to be effective, must have a goal. In the writings of some authors the analogy between ontogeny and an orthogenetic racial life is carried to the point where senescence and death seem to be the goal of each segment of the evolutionary tree. But the highly complex environmental situation of stirps is constantly changing and the end by extinction, as contrasted with extermination (see Tolmachoff, 1928), cannot be safely predicted.

When only two forms in a presumed ancestral-descendant sequence are known, a straight line on a diagram is the shortest, most orderly, and most economical distance between them. Adjacent names of the elements of even the longest and most branching phylogenies are frequently treated this way for diagrammatic and conventional simplicity, and for the same reasons a line is straightened through the entire sequence of the group under discussion. Straight lines in nature or its discussion suggest laws. The tyranny of diagrams has probably been a real factor in the uncritical part of the popularity of orthogenesis.

Orthogenesis has often been appealed to for a rationalization about the beginnings of structures which are presumed to be useless in incipient stages, as mentioned above. Some structures which are frequently placed in this department of orthogenesis, such as the rattle of rattlesnakes and the "sail" of the Permian sail-lizards, can perhaps be better rationalized when we revise our notions of function.

Quite probably the rattlesnake's rattle is not primarily a warning device, which is functional only when fully developed, but is rather a lure which is effective in its smallest development, with signals to the eyes, the nose, and the ears of potential prey. Many suggestions, some nonsensical, for the adaptive utility of the long vertebral spines of pelycosaurs have been made and discarded. The so-called sails could not have been effective as protection, as camouflage, or literally as sails. For two generations the function

has been inexplicable and some authors have simply abandoned the problem by "explaining" that the sails "represent an unbalanced growth" or are an example "of heredity gone wild." Some years ago, however, a review of the climatic and taxonomic situations of pelycosaurs by a student for a seminar report led to the idea that the sails were thermal regulators, a suggestion which recently has found support in the great abundance of haversian canals in the neural spines of the high-sailed pelycosaurs. This same thought, that the sails would have been effective in absorbing or giving off heat, is stated by Romer (1949: 104) to have been suggested later and quite independently to him, and he discusses its implications in terms of adaptation.

Orthogenesis has been alleged to be responsible not only for the beginning of characters but for their development, by "momentum" or other means, to the point where they cause "overspecialization" and extinction. Favorite and hackneyed examples are the sabre-toothed felines, the "Irish elk," the dinosaurs, the trilobites, the ammonites, and the grypheas. The literature about each is voluminous and repetitious and the conclusions of authorities apparently have little effect upon the persistence of certain superstitions or fictions.

Matthew (1910: 306–307) discussed the notion of momentum as a theory to account for extinction and said that

> Those who have advocated this, to me impossible, theory have repeatedly quoted *Smilodon* as an example in support. In point of fact . . . the immense development of the canines in this animal made them highly efficient weapons for a mode of attack and was an essential element of its success in its especial mode of life, not a hindrance or bar to its survival. Whatever may be thought of the theory of "momentum in evolution," *Smilodon* cannot be used as an instance in its support.

Matthew's protest was against such statements as had been made by Loomis (1905) and Woodward (1909) in their uncritical citations of the machaerodonts as an example of specialization beyond utility. More recently this subject has been discussed by Lull (1939) and by Romer (1945) who retain the suggestion that the long canine was used in stabbing and killing large prey whose demise doomed the killers, but Bohlin (1940) did not think much of the stabbing hypothesis and "even would go so far as to denounce it" in favor of carrion feeding.

As a matter of fact much of the argument about progressive "overspecialization" of the sabre-toothed cats, at least as far as the teeth are concerned, is quite beside the point because the canine teeth of the earliest known members of the group were relatively, in proportion to skull size, as large as those of the last survivors.

Despite the fact that the notion of "momentum" is usually stated to be a bias of paleontologists, in connection with discussions of orthogenesis, there are more speculations about it by neontologists. Among paleontologists who favored the idea were Beecher (1901: 58), who wrote of a law which ". . . may carry a structure beyond the bounds of efficiency," and Loomis and Woodward (noted above). Matthew (see above) strongly discounted "momentum," as have many other paleontologists. Among neontologists the following have proposed interesting ideas about what is sometimes called "evolutionary inertia" and is usually based upon hearsay about the paleontological record. Haldane (1932: 23), says that "One is left with the impression that the evolutionary process somehow acquired a momentum which took it past the point at which it would have ceased on a basis of utility." Huxley (1944: 38) in a weak estimate of the value and limitations of paleontology observes that all assertions about ". . . inner momentum which in technical parlance is called orthogenesis . . ." as the prime cause of evolution are unjustified on the score of simple logic and scientific method. On page 173, however, he says that ". . . it is possible that orthogenesis may in some cases be at work." He had written this same conclusion in 1940 (pp. 11–12) about admitting "a little orthogenesis" because ". . . it is difficult . . . to account for certain deleterious trends . . . without appealing to some degree of internally directed evolution. . . ." Howells (1944: 79) says that

> Many ascribe the growth of the brain to still another principle, which is especially impressive to paleontologists studying animal lines through long periods of their history: this is orthogenesis, or the unexplained fact that certain features may develop along a straight line, with a momentum and exaggeration which can hardly be put down to natural selection.

Metcalf (1928: 35) writes that "It is *momentum of mutation* that is the chief idea in this paper, the habit which mutations so often show of starting a trend." In 1939 (p. 52) Wright suggested that there are certain minor trends ". . . which strongly suggest a sort of organic momentum."

Many attempts, none apparently wholly satisfactory, have been made to learn why various

cervoids have antlers. These bony growths, usually confined to the males, have been called weapons for offense and defense in mating and other struggles, ornaments for sexual attraction, snow picks or shovels, the results of irritating impacts, structures which are accidentally and incidentally linked to gonadal developments, hearing-aid devices, and the results of heterogonous growth (allometry, which explains almost nothing). The "Irish elk" (a deer) apparently had larger antlers, in terms of body size, than any other known ungulate. Because it is also extinct large antlers and extinction are classically linked as cause and effect. It is by no means certain, however, that this is a correct interpretation, or that any of the suggested functions for antlers are the primary ones. Perhaps it is the "velvet" stage of antler growth which is significant in metabolic and sexual adaptation, or there may be other physiological attributes which have not been perceived. In short, neither the function of antlers nor the cause of extinction of *Megaceros* is wholly known. Nor does anyone know why dinosaurs and ammonites and grypheas and trilobites became extinct. Many authors have speculated about senescence, degeneration, momentum, and orthogenesis as causes although some paleontologists, who might be presumed to have first hand knowledge of these groups, have resoundingly rejected such speculations.

After a considerable search I have not found among vertebrate fossils a single apodictic example of orthogenesis in either the descriptive or the theory sense. Each case that has been called orthogenesis seems to be at least as well described or explained by other figures or theories. Many sequences, however, have been regarded as examples of orthogenesis at some stage in our information (or ignorance) about them. As an example the apatemyids may be cited (see Jepsen, 1934). They were small (marmoset-sized), relatively big-brained Early and Mid Tertiary primates. A few years ago, after a long history of cumulative evidence and of vacillating notions, we knew that apatemyids ranged from the Late Paleocene to the Early Oligocene and the simple unbranched American distribution was, from earliest to latest genera, *Labidolemur, Teilhardella, Apatemys, Stehlinella,* and *Sinclairella.* Each genus except one was represented by a single species and the exception, containing two nominal species, may be merely a dimorphic pair within a single species. Apatemyids are very rare. Most species are represented by single specimens which, however, have come from strata that yield large samples of other populations.

At this stage of information the group made a fair example of the kind of "orthogenesis," although it was never cited as such, that is found in the literature more than in nature. Soon, however, the line on the diagram of the apatemyids was extended by the discovery of a Mid Paleocene form and then by another, which gave a choice of ancestry for the Late Paleocene group. And recently, representatives of two other genera have turned up and are the contemporaries of Eocene species. At present, therefore, the family tree of the apatemyids is sprouting roots and branches and cannot be longer visualized as a single straight stalk or trend.

Study of the extinct apatemyids illustrates on a small scale the history of accumulation of knowledge about other lineages, including that of the horse which has been so earnestly cited as proof for so many notions, particularly for orthogenesis. Unfortunately the newest observations by specialists on the evolution of the horse take a long time to become generally known. Many recent comments about equine history seem to be based, with minor revisions, upon the record as it was known (see Cope, 1887*a*: 1075) even before the word orthogenesis was devised. At present the chart of horse evolution is a bushy tree with many side branches (see Stirton, 1940, 1947; Edinger, 1948; Romer, 1945, 1949). For approximately a decade authorities on paleontology have insisted that the modern pattern of horse evolution is not a straight-line trend and that it cannot be cited in any way as evidence for orthogenesis. Popularly, however, and in some scientific quarters as well, horse evolution is still a simple matter of description and theoretical orthogenesis. As an exasperated paleontologist recently remarked "There is a tendency to put the chart before the horse."

It is worthy of note that, recently, few of the most extreme advocates of orthogenesis have been vertebrate paleontologists, although there are some notable exceptions. Most of the all-or-none school are biologists or botanists. To Griggs (1939: 136) ". . . whether we understand it or not, orthogenesis must be accepted as the way of evolution," and to Schaffner (1928*a*: 291, and in many other later spots in his writing) "Evolution is intrinsic, kinetic, orthogenetic, perfective, and determinative."

Rensch (1947) lists paleontologists and biologists who favor and accept orthogenesis, Teichert

(1949) cites invertebrate paleontological writings in support of the theory, and Berg (1926: 149) names writers who have "declared in favor of orthogenesis." Among paleontologists who have declared against orthogenesis except as a descriptive term are Colbert (1949, .1949*a*), Dunbar (1924, and 1932, in reference to Fenton 1931, on spirifers), Jepsen (1943), Romer (1945, 1949), Simpson (in press and in earlier papers), and Wood (1938, 1949). Osborn's writing had a great influence, particularly among biologists, and, although it is hard to understand him now, he was presumably firmly in favor of orthogenesis, usually under different names (see especially Osborn, 1922).

Considering these authors and many others in a recent (and incomplete) census of opinion about orthogenesis, it may be said in summary that, as usual, opinion is divided. At a later date this tabulation may be completed along with a survey of the extensive literatures upon hybridization and parallelism and phylogenetic increase in size of organisms (see, e.g., Newell, 1949) as factors in evolution because these subjects are closely related to concepts of orthogenesis and are now being actively developed.

Allometry, or differential rates of growth of parts, or the effects of rate genes and linkages are among current descriptions or explanations for some of the phylogenetic sequences and parallelisms which were formerly described as orthogenetic, but they have little real explanatory content.

Paleontology, as known to me, supplies no unequivocal evidences for a theory of orthogenesis or momentum controlled by internal or external drives. The evidence seems rather to support the idea of orthoselection (Plate, 1913; and see, also, Rensch, 1947; Romer, 1949; and Simpson, 1944 and in press) wherein natural selection eliminates certain genetic or biochemical elements and provides the opportunities for others to develop and change and thus, in a sense, to channelize progressive evolution.

There are, however, a very great many unanswered questions.

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REALITY AND EFFICACY OF SELECTION IN PLANTS[1]

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SINCE the classic work of Darwin, no serious minded scientist has doubted that natural selection exists as a factor in evolution. There has, however, been wide divergence of opinion on the importance of this factor, and since the rise of modern genetics many students of that branch of biology have tended to regard selection as a purely negative force, eliminating the obviously unfit individuals, but not taking part in the creation of any new types of organisms. Although proponents of this point of view have existed among both plant and animal geneticists, the most widely cited and apparently most convincing evidence has come from the higher plants. Most important in this connection is the work of Johannsen in beans, and that of de Vries on mutations in *Oenothera*.

Johannsen demonstrated that in a self-pollinated plant like the garden bean the limits of selection are reached in a very few generations with the establishment of a completely homozygous pure line, and that in organisms of this genetic constitution natural selection cannot be expected to have any appreciable effect. De Vries showed that in another largely self-pollinated plant, *Oenothera lamarckiana*, apparently new types arise suddenly, and some of these breed true at once. The combination of these two discoveries led rather naturally to the idea that new types arise not by the accumulation of small hereditary variations, guided by the action of selection, but by sudden jumps; the new types being accepted or rejected as wholes whenever they arise. Once this idea became widespread in botanical literature, including the elementary text books, botanists who still believed that natural selection was a major guiding force in evolution were placed on the defensive, and for many years during the beginning of this century even experiments designed toward demonstrating the role of natural selection were not considered a fit occupation for experimental botanists. This attitude is now beginning to change, but the change is coming as much through influence from biologists dealing with animal material, such as Fisher, Wright, Dobzhansky, and Muller, as from new discoveries on the part of botanists themselves.

It was not an accident that the factual data which seemed to go against the selection theory as proposed by Darwin were obtained from plants. In animals, cross fertilization is the rule, every individual is more or less heterozygous, and pure lines are unknown and impossible to obtain. Self fertilization is, on the other hand, relatively frequent in the higher plants, and particularly so in those plants which form the most suitable material for experiments on plant breeding and genetics, namely the annual grains, vegetables and flowers commonly grown in the garden and field. In such plants, pure lines are to be expected, and abrupt alterations of the hereditary characteristics would be particularly easy to detect. However, these groups are not typical of the higher plants. Study of the wild relatives of the self pollinated crop and garden plants shows that many or even most of these relatives and presumable ancestors are regularly cross pollinated, often being self incompatible. Hence they are highly heterozygous and do not form pure lines. Furthermore, numerous studies of inheritance in crosses between different wild races and species of plants have shown that most of the character differences between them are inherited according to the principles of multiple factor inheritance, and so have probably arisen not through the occurrence and establishment of single mutations with large effects on the phenotype, but through the accumulation of many small mutational steps. From these facts, we may conclude that evidence obtained entirely from self fertilized crop plants, and from organisms like *Oenothera*, which is both self fertilized and cytologically very abnormal, can give us a very misleading picture of the forces which have stimulated and guided evolution in the plant kingdom as a whole. In the present article, therefore, both the older and newer evidence from crop plants will be balanced against that obtained from wild species in an attempt to

[1] Much of the material in this paper is presented in a somewhat expanded form in a book, *Variation and evolution in plants*, by the present author and being published by the Columbia University Press.

obtain a more complete and well rounded picture of the role of selection in plant evolution.

THE LIMITS OF ARTIFICIAL SELECTION

As a contrast to the results of Johannsen on pure lines of the self fertilized garden bean, we now have available the results of five long continued experiments on artificial selection in cross fertilized organisms, four on animals and one on plants. All five of them have yielded essentially similar results. That of Goodale on mice and those of Payne, Sismanidis, and Mather on *Drosophila* deal with animal material and so will not be discussed here. The fifth is the large scale experiment which has been conducted for nearly fifty generations at the University of Illinois on maize. There is only one publication on this experiment: that of Winter (1929), which records the results obtained during the first twenty-eight years. The most significant data up to 1947, forty-eight generations after the inception of the experiment in 1896, have been kindly supplied to the writer by Professors C. M. Woodworth and O. T. Bonnett of the University of Illinois.

Although maize is a cultivated crop plant, it is nevertheless normally cross fertilized, and in the Illinois experiment both selfing and too close inbreeding have to be avoided in order to keep the lines from degenerating in vigor. Artificial selection is being carried on for four characteristics, high and low content of protein in the grains, and high and low oil content. Some of the results are presented in table 1. The mean protein content, which was 10.93 per cent in 1896, had been raised in the high protein line to 16.6 per cent in 1924 (Winter, 1929), and by 1946 had reached 20 per cent. In the low line, protein content had been reduced to 8.38 per cent in 1924, and 5.11 per cent in 1947. It is notable that in this characteristic the reduction had been greater during the last twenty-three years than during the first twenty-eight. Oil content was raised in the high oil line from 4.68 per cent in 1896 to 9.86 per cent in 1924 and 15.45 per cent in 1947; again a greater change in the last twenty-three years than earlier. In the low oil line, oil content in 1947 had been reduced to 0.76 per cent, one-twentieth of that in the line selected for high oil content.

TABLE 1

SOME RESULTS OF SELECTION FOR HIGH AND LOW CONTENT OF PROTEIN AND OIL IN KERNELS OF MAIZE

(Data from the Illinois Agricultural Experiment Station)

Year and duration of experiment	Mean protein content in per cent		Mean oil content in per cent	
	High protein line	Low protein line	High oil line	Low oil line
1896 (0 yrs.)	10.93	10.93	4.68	4.68
1924 (28 yrs.)	16.60	8.38	9.86	1.51
1940 (44 yrs.)	19.92	6.19	12.57	1.36
1947 (48 yrs.)	19.24	5.11	15.45	0.76

The response to selection in both this experiment and the ones on *Drosophila* was not one of even progress, but rather of successive spurts, between which were periods of several generations during which selection had little or no effect. On first sight, this might seem to favor the view that the success of these experiments was due to the fortunate appearance of mutations with a large effect on the characters being selected. However Mather and Wigan (1942), in their experiments on selection for high and low number of abdominal chaetae in *Drosophila melanogaster,* performed the critical experiment of selecting for high number among certain individuals of a line which had previously been selected continuously for low number, and in that way obtained results which are very difficult to explain on the hypothesis of the occurrence of a few mutations, each with a conspicuous effect. Furthermore, they showed that the data are more easily explained on the basis of another hypothesis, namely that the periods of sudden change are due to the appearance of favorable combinations of "polygenes," or genes which individually have relatively little effect on the phenotype. Many of these genes are presumed to have been in the original stocks before selection was begun, but some probably represent mutations which arose during the course of selection. Their sudden appearance as favorable combinations is probably due to the effects of linkage and crossing over. As yet nobody has performed the critical experiment necessary for testing this hypothesis, namely crossing a line selected for a high value for a given character with a low value line for the same character. This critical evidence should be obtained in the not too distant future.

There is, moreover, additional evidence that natural selection could operate continuously through the occurrence and establishment of combinations of mutations with small effects. This is derived from observations by some geneticists that such small mutations occur much more frequently than the more conspicuous ones. The

TABLE 2

SURVIVAL OF BARLEY VARIETIES FROM THE SAME MIXTURE AFTER REPEATED ANNUAL SOWINGS AND COMPETITION OF VARIOUS DURATION (Condensed from Harlan and Martini, 1938)

	Arlington, Va. (4 yrs.)	Ithaca, N. Y. (12 yrs.)	St. Paul, Minn. (10 yrs.)	Moccasin, Mont. (12 yrs.)	Moro, Ore. (12 yrs.)	Davis, Calif. (4 yrs.)
Coast and Trebi*	446 T	57 T	83 T	87	6	362 C
Hannchen	4	34	305	19	4	34
White Smyrna	4	0	4	241	489	65
Manchuria	1	343	2	21	0	0
Gatami	13	9	15	58	0	1
Meloy	4	0	0	4	0	27

* The records on these two varieties were combined because of the difficulty of distinguishing between their seeds. The figures marked T indicate a predominance of Trebi, those marked C, a predominance of Coast.

first to make such an observation was Baur (1924), who found that self pollinated lines of *Antirrhinum* never became completely constant, and estimated the percentage of small mutations in them to be as high as 10 per cent. East (1935) made similar observations on a homozygous diploid line of *Nicotiana rustica* which had been obtained by doubling the chromosome number of a haploid. That these small mutations are by no means universal was demonstrated by Lindstrom (1941) who found that a homozygous diploid line of the garden tomato obtained from a haploid was completely uniform after nine generations of selfing. The occurrence and frequency of small mutations is one of the most important unexplored fields of genetics in its relation to evolution. It should be attacked in fungi and other lower plants, because of their rapidity of reproduction, the large number of plants which can be grown in a relatively small space under uniform conditions, and particularly because many of them are haploid, so that all mutations would have an immediate effect on the phenotype.

At present, we are nevertheless justified in assuming, as have many biologists, that natural selection acts for the most part not on individual mutations as they arise in the germ plasm, but on the combinations of old and new mutations which occur during the segregation and recombination processes which are characteristic of sexual reproduction. We come at once, therefore, to the assumption that the relationship between mutation and selection in evolution is an indirect rather than a direct one. This assumption will appear more and more justified as we review other evidences of the action of selection.

We can conclude this section, therefore, with the statement first that the limits of selection in a cross-breeding population are not yet known, and for many characters definitely not reached after fifty generations. Furthermore, selection, both artificial and natural, will in most instances sort out primarily gene combinations and therefore only indirectly affect the frequency of individual genes.

EXPERIMENTS ON COMPETITION AND NATURAL SELECTION

The reality of natural selection as a guiding force in evolution can be shown most clearly by means of experiments in which the environment is permitted to sort out genotypes from a mixture, or from a heterozygous, cross-fertilizing population. Ideally, these should be carried out under conditions essentially the same as those existing in nature and should use material of known genetic composition in a cross-fertilizing, diploid organism. These conditions, however, are very difficult to fulfil in actual practice, and no such ideal experiment has yet been performed. Four experiments will be cited, however, which approach this ideal.

The first and most extensive of these was by Harlan and Martini (1938) on cultivated barley (*Hordeum vulgare* L.). They planted a mixture containing equal quantities of seed of eleven different commercial varieties of barley in each of ten different experiment stations located in various parts of the United States. The crop obtained from this mixture was harvested in bulk at each station, and a random sample of 500 seeds was extracted. The number of seeds of each variety was counted for such comparable samples at each station. Part of the remainder of the mixed harvest was planted the following spring under the same conditions. The experiment was carried on for periods varying from four to twelve years, depending on the locality.

Table 2 shows a part of the results obtained. Selection has clearly taken place, since in nearly every station one variety was strongly predominant, and the dominant variety differed according to the locality. Two other facts are also significant. In the first place, the number of varieties which survived was relatively large in some localities, such as Moccasin, Montana, but much smaller in others, such as Moro, Oregon. Secondly, the individual varieties differ greatly in their ability to tolerate a variety of climatic conditions. For instance, the variety Hannchen, though dominant only at St. Paul, Minn., survived at least in small percentages at each locality. On the other hand Manchuria, which was highly successful at Ithaca, N. Y., was a failure at nearly every other locality.

To the student of general evolution, the value of this experiment lies in the analogies which may be drawn from it. Many wild species are known which are rich in genetic variants in some localities, known as gene centers (Turesson, 1932), and are much more uniform genetically in others. The results of Harlan and Martini show that such differences in genetic variability could be produced in barley in relatively few years by natural selection alone, and therefore do not support the hypotheses of geneticists and plant geographers who would attach historical significance to gene centers, considering that they may be the localities in which the species originated. Furthermore, the fact that some barley varieties have a greater ability than others to tolerate widely different climates suggests that a wide range of tolerance, and therefore a wide geographic distribution, may be acquired by a species both through the possession of a wide variety of different genotypes and through the existence of certain individual genotypes which by themselves have particularly wide ranges of tolerance.

Harlan and Martini also provided data on the rate at which the unsuccessful and partly successful varieties became eliminated or reduced in number. They pointed out that in a group of competing varieties differing from each other to equal degrees as to their competitive ability, the most successful ones would rise rapidly and rather evenly throughout the experiment on competition. Those of intermediate adaptive value would rise rapidly at first, reaching a rather low peak, then decline equally rapidly, but the rate of decline would slacken toward the end of the experiment. Finally, the unsuccessful types would decline rapidly at the beginning of the experiment, and then more slowly, so that some of them would retain a very small number of individuals for many generations. These changes are based on principles similar to those worked out by Fisher (1930) and Haldane (1932) for the survival of alleles in a heterozygous population. That the expected changes were realized in Harlan and Martini's experiment can be seen by comparing figures 1 and 2. These results help us to understand how natural selection would produce a situation well known to botanists, namely that in many if not most groups of plant species the majority of the rare, endemic species are relics which formerly had wider ranges of distribution. They have survived largely in places where competition has been relatively little, and selection not very rigid.

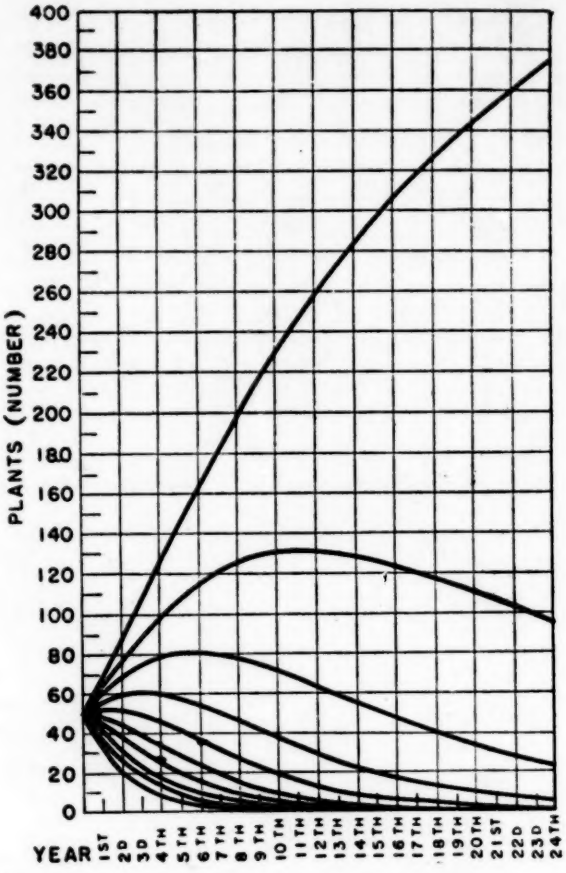

FIG. 1. Theoretical curves of natural selection based on an equal mixture of 10 varieties of cereals differing by 5 kernels each in their productivity per plant, the poorest plant producing 45 kernels.

The fact must be emphasized that this experiment on competition between varieties of cereal grains is radically different from one which might

be conducted on a typical wild species, particularly in the fact that barley is predominantly self fertilized, and selection is on the basis not of genes but of whole genotypes or biotypes. Similar experiments are needed, using material of a cross-fertilized species.

Experiments which show the short-time effectiveness of natural selection in a cross-fertilizing plant species are those of Sylvén (1937) on clover. He showed that strains of white clover (*Trifolium repens*) originating from Denmark and Germany, when planted in the more severe climate of southern Sweden, became adjusted to this climate over a period of two years through selective elimination of the less hardy individuals, with the result that yields of green matter increased markedly (table 3). This increase, however, was confined to varieties (Morsø and the German strain) which had not previously been subjected to artificial selection, and were therefore relatively diverse and heterozygous in their genetic composition, while the more highly selected, homozygous strain Strynø did not respond to the change in climate.

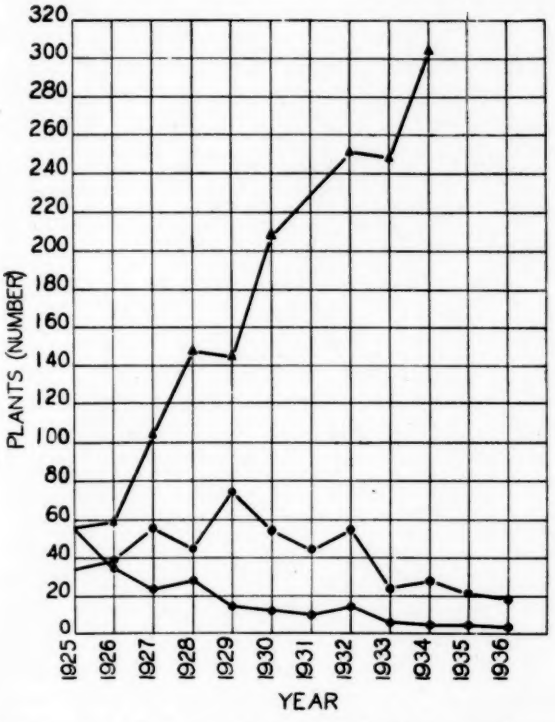

FIG. 2. Actual curves showing the change in number of plants of representative varieties of barley initially sown in equal quantities in a mixture. Triangles, a dominant variety, Hannchen at St. Paul, Minn., solid circles, a better than average variety, Hannchen at Moccasin, Mont., open circles, a poor variety, Meloy at Moccasin, Mont.

TABLE 3

YIELD OF GREEN MATTER (RELATIVE FIGURES) OF DIFFERENT WHITE CLOVER STRAINS AT SVALÖF

(Data of G. Nilsson-Leissner, from Sylvén, 1937)

Strains	Directly imported seed	Seed from first generation at Svalöf	Seed from second generation at Svalöf
Morsø	100.0	106.6	115.5
Strynø	100.0	100.3	102.4
German strain	100.0	129.1	137.2

Sylvén obtained similar results in plantings of red clover (*T. pratense*) in southern and central Sweden. Plantings made in southern Sweden, where the diseases clover stem rot and clover eel worm are prevalent, developed resistance to these diseases in one generation owing to elimination of susceptible individuals; while seed from the same source grown in central Sweden, where these diseases cannot develop owing to the more severe winters, failed to develop resistance. These experiments, and many others like them, show not only that natural selection is a powerful force in changing plant populations, but also that it must be reckoned with in agricultural experimentations.

An experiment demonstrating how natural selection might act in a cross-fertilizing wild species is that of Clausen, Keck, and Hiesey (1947) on a hybrid population derived from crossing two subspecies of *Potentilla glandulosa*. One of these (subsp. *reflexa*) came from the Sierra foothill area of California, a region with mild, rainy winters and hot, dry summers, while the other (subsp. *nevadensis*) grew naturally at timberline in the high mountains, where the growing season is restricted to hardly more than two months in the summer, but where moisture during this season is abundant. The highly fertile F_1 hybrid between these two subspecies yielded a large, strongly segregating F_2 population, from which 575 individuals were each divided into three clonal divisions, one of which was planted in each of their three experimental gardens; at Stanford, in the coastal region of California, at Mather, in the Sierra Nevada at 4700 ft. (1400 m), and at timberline (3050 m) in the Sierra Nevada. Over a period of five to eight years some of these individuals were eliminated at each station, and in most cases these were different. On the other hand, some of these segregating F_2 genotypes showed the unexpected ability to survive and produce seed at all three stations, which was not

true of either of their original parents. Although only one generation was tested in this experiment, it shows strikingly the results which might be expected from one of the same nature continued over several generations.

The final experiment to be mentioned is one by the present author on competition between a diploid species of grass and the autotetraploid derived from it artifically through colchicine treatment. It is described elsewhere in greater detail (Stebbins, 1949). Seeds or plants of diploid and autotetraploid *Ehrharta erecta* Lam. were planted in ten different sites on or about the campus of the University of California, Berkeley, in the autumn of 1943. Four and one half years later, in the early summer of 1948, at least the diploid strain had spread considerably in eight of these localities through natural seeding. The tetraploids, however, reproduced themselves in only four of these plots. Nevertheless, there was one plot in which the tetraploids spread more rapidly than the diploids, so that in 1948 this plot contained 185 plants of the tetraploid and only 26 of the diploid. A highly significant fact is that this plot was on a very different site from the others, namely a steep, well drained hillside on which the soil became drier during the summer than in any of the other localities. In a second locality where the number of tetraploids is increasing, although they are far fewer than the diploids, the tetraploids are confined to a portion of the plot which also is a hill crest with good drainage. In this experiment, therefore, different ecological preferences of these two chromosomal types, one derived from the other under experimental conditions, are becoming revealed in as short a period as five years. Furthermore, these differences would probably not be very great in terms of geographical distribution. Plantings of diploid and autotetraploid *E. erecta* made in Monterey County, 120 miles south of Berkeley in a region with about the same annual rainfall and a somewhat similar flora, were either completely unsuccessful because the plants failed to survive the dry summers, or in moister sites resulted in a rapid spread of diploids at the expense of tetraploids, just as in the majority of the sites at Berkeley. This experiment, though not wholly satisfactory in itself, points the way to the conduction of similar experiments in material which is undergoing genetic segregation, and which will therefore more nearly simulate the action of selection on natural panmictic populations.

NATURAL SELECTION, GENE ACTION, AND ADAPTATION

The experiments discussed in the previous section, along with similar and much more abundant evidence from animals, leads to the conclusion that all differences between races, species, genera, families, or any other groups of plants which are adaptive or connected with adaptation have evolved through the guidance of natural selection, acting on gene recombination and mutation. The central problem of the efficacy of natural selection in producing the diverse groups of organisms which exist on the earth depends very largely, therefore, on the extent to which the differences between these groups are connected with adaptation. Before this problem is considered, however, the probability must be emphasized that many of these differences, although they do not have a direct adaptive value as single characters, nevertheless have been established wholly or partly through the indirect influence of natural selection, because of the relation between these characters and others of direct selective value. An understanding of the indirect action of natural selection may be obtained by studying three processes through which it works, *developmental correlation, adaptive compensation,* and *selective correlation.*

The principle of developmental correlation was well recognized by Darwin, and mentioned several times in the *Origin of Species.* In terms of modern genetics, it can be stated about as follows. The direct action of genes is on the processes of development and metabolism; hereditary differences between adult individuals in visible characters are produced indirectly through the effects of genes on developmental and metabolic processes. Because of this fact, character differences which are affected by the same developmental or metabolic process are necessarily correlated with each other since they are influenced by the same genes. This is the basis of most if not all of the phenomena which have been termed by geneticists pleiotropy, or the production of manifold effects by a single gene.

A large series of genes with multiple effects which are probably due to developmental correlation has been described by Anderson and De Winton (1935) in *Primula sinensis.* Some of these genes affect only the floral parts; others alter the shape of most or all of the organs; leaves, bracts, calyx lobes, corolla lobes, and ovary. Any one gene produces similar effects on different

organs, so that these are best explained by assuming that each mutant alters some specific development process. This process may take place in the development of only one organ, or it may be repeated in slightly different form in most or all of the different organs of the plant. The degree and the nature of the alteration in each organ depends as much on the character of the developmental processes in that organ as on the nature of the gene itself.

An example of developmental correlation involving genes which govern the differences between species is provided by segregates from the hybrid *Nicotiana alata* × *Langsdorffii* (Anderson and Ownbey, 1939; Nagel, 1939). *N. alata* is larger in all of its parts than *N. Langsdorffii;* this is the result of a greater cell size. Certain parts, particularly the leaves, bracts, and corolla tube, are more elongate in *N. alata;* this results from the greater ability of the cells of this species to utilize growth hormones.

The effects of such correlations on the alteration of characters by natural selection are undoubtedly very great, but are practically unexplored. If, for instance, long roots should, because of a change in the environment, acquire a high selective value in one race of a species, mutations producing cell elongation in the roots would become established in that race. Some of these mutations would almost certainly affect cell elongation in leaves and flowers, and would therefore produce interracial differences in respect to these parts. In plants, which produce serially large numbers of similar organs, developmental correlation is to be expected with particularly high frequency, and it is very likely responsible for the origin by selection of many character differences which by themselves have no selective value.

The principle of adaptive compensation, the importance of which was recently suggested by Clausen, Keck, and Hiesey (1948), is a direct consequence of the effects on selection of developmental correlation. A gene or series of genes may be favored by selection because of one of their effects, but other effects of the same genes may be disadvantageous to the organism. Under such conditions, still different genes which tend to compensate for the harmful effects of the original ones will have a high selective value. An example of this type is provided by Tedin's (1925) analysis of genetic differences between races of the weed, *Camelina sativa*. This species has evolved races which inhabit flax fields, and which "mimic" fibre flax in their erect, unbranched habit, relatively few flowers, and particularly their large, light seeds. Selection for increased seed size has been particularly intense in the evolution of these races, since the only seeds of *Camelina* which become planted are those sufficiently like the seeds of flax to become mixed with them during the winnowing process. Tedin found that genes for increased seed size automatically reduce the number of seeds per pod, through developmental correlation. Nevertheless, the large seeded, flax-mimicking races of *Camelina* have as many seeds per pod as their smaller seeded relatives. This is because they possess also genes for increased size of pods which have no effect on seed size but serve independently to increase the number of seeds per pod. Increased pod size is not by itself a character of particular selective value in these races of *Camelina,* but has been established by selection because it compensates for the tendency toward decreased seed production which is the effect of the genes for increased seed size.

Once a group of genes has been established in a race because of their role in adaptive compensation, they and the initially valuable genes form an adaptive system which must be maintained as a unit if the race or species is to retain its adaptiveness. As Tedin has pointed out, groups of characters will be kept together by selective correlation. The relation between these three important secondary effects of selection may therefore be stated as follows. Developmental correlation brings about adaptive compensation which results in selective correlation.

One of the most important features about adaptive compensation and selective correlation is that compensation may be brought about in many different ways. For instance, Tedin found that two different flax-inhabiting races of *Camelina* both had large pods, but differed principally in pod shape. In one of them the genes for increased pod size acted chiefly to increase the length of the pods, but in the other the size genes which had become selected caused an increase in their breadth and thickness. The two races, therefore, had diverged from each other in the shape of their pods through the influence of a single selective agent, because the available genes for adaptive compensation had presumably been different when selection for seed size began. There is good reason to believe that many of the differences between species, genera, and families of plants are in characters which have evolved through selective correlation because they compensate for certain ill effects of otherwise adaptive genes.

As has recently been emphasized by Salisbury (1942), the adaptive value of seed size varies greatly with the habitat of the plant. We can imagine, therefore, that under a number of different circumstances plant species would be exposed to habitats in which large size of seeds would have a high selective value. This would favor the establishment of genes for increase in seed size and decrease in number of seeds per pod or carpel. Compensation for reduction in reproductive potential thus caused could be brought about either by increasing the size of the pods or carpels, as in *Camelina*, or in any of a number of other ways, such as increase in number of carpels per flower, of flowers per inflorescence, or of inflorescences per plant. Since the particular method of compensation which became adopted by any race would be determined largely by those mutations which happened to be present in its germ plasm at the time when selection for seed size began, different races of the same species, living in different regions, could diverge from each other under the influence of the same selective pressure, through the establishment and further selection of different mechanisms for adaptive compensation. They would come to differ not in characters of direct, easily demonstrable selective value, but in characters of indirect, though of no less vital significance, established as methods of adaptive compensation, and maintained through selective correlation.

Adaptive compensation and selective correlation are not confined to the interrelationships between different characteristics of the same organ, or even between organs with similar or related functions. Often differences between the vegetative organs and habit of growth of related species are correlated with those involving the reproductive organs. Two conspicuous examples can be given.

One of these is in the wheat or barley tribe of the grass family (tribe Hordeae, family Gramineae). The species of this tribe, about three hundred in number, can be divided artificially into three groups as to their general habit of growth. Some of them are perennials with well developed underground stems or rhizomes, as in the common quack grass (*Agropyron repens*). In these, because of their very efficient method of vegetative reproduction, the individual genotype is not only very long-lived, but in addition can spread over a large area. Consequently, one would not expect efficient reproduction by seed to have a high selective value in such species. Other species are perennials, but lack rhizomes, so that a particular genotype is confined to one spot, although it may live there for a long time. In them, one would expect the selective value of efficient reproduction by seed to be higher than in the rhizomatous perennials, and to vary considerably depending on the length of life of the plant and the habitat in which it grows. Finally, many species of the tribe are annuals which live for only a single season and depend entirely upon seed for the maintenance of the line. In these, we should expect efficient seed dispersal to have a particularly highly selective value.

The species of the tribe also show great differences in the structure of their reproductive parts, chiefly their inflorescences. Most of these differences are related to different methods of seed dispersal, some of them highly efficient, others less so. Among the most frequent of them are those in the shape and degree of elongation of the sterile scales or glumes, in the length of the terminal awn of the fertile scale or lemma, and in the character of the rachis of the inflorescence. Elongation of both glumes and lemma awns facilitates dispersal of the seeds by animals. Another character with the same type of selective value is the presence of joints or articulations at the nodes of the rachis of the inflorescence. These make the rachis fragile, so that at maturity it breaks up into several sections, each containing one or more spikelets, with their groups of seeds and sterile scales.

Table 4 shows the relationship between the growth habit and the type of seed dispersal mechanism in those species of the tribe which occur in

TABLE 4

RELATION BETWEEN GROWTH HABIT AND SEED DISPERSAL MECHANISMS IN 215 SPECIES OF THE GRAMINEAE, TRIBE HORDEAE

	Rhizomatous perennials	Caespitose perennials	Annuals	Total
Awn shorter than lemma, glumes not elongate	48	59	6	113
Awn longer than lemma, glumes not elongate	4	56	7	67
Awn usually longer than lemma, glumes aristate, elongate	0	18	17	35
Total	52	133	30	215
Rachis continuous	52	115	3	170
Rachis fragile	0	18	27	45
Total	52	133	30	215

the United States, the Soviet Union, and the eastern Mediterranean region. These regions include the main area of distribution of the tribe, and their species are well described in three floras, Hitchcock's (1935) *Grasses of the United States,* volume II of Komarov's (1935) *Flora of the U.S.S.R.* and Boissier's (1875) *Flora Orientalis,* from which the data for table 4 were obtained. This table shows clearly the expected correlation between shortness of life cycle or lack of vegetative reproduction on the one hand, and efficiency of seed dispersal on the other. The correlation is even more complete than is shown by the table. Within the large group of caespitose perennials, those with particularly vigorous vegetative growth and long life, such as *Agropyron cristatum, A. elongatum,* and *Elymus condensatus,* have relatively poorly developed methods of seed dispersal, while smaller, shorter-lived types, like the perennial species of *Hordeum* and *Sitanion,* have as highly developed mechanisms for seed dispersal as do many of the annuals.

In the genus *Crepis* there is a similar inverse correlation between longevity and efficiency of seed dispersal. Babcock (1947) has arranged the 196 species and 27 sections of this genus in order of increasing specialization of their involucres and achenes, this specialization being associated primarily with more and more efficient seed dispersal. He has found that the least specialized in these respects are the rhizomatous perennials, while the tap-rooted perennials are intermediate and the annuals most advanced, just as in the grasses. In the genera related to *Crepis,* such as *Prenanthes, Lactuca, Sonchus,* and *Hypochaeris,* the writer has found the same relationship to hold, and it doubtless exists in other groups.

All of this evidence leads to one conclusion; that natural selection in the higher plants is based on harmonious, adaptive combinations of characters, and that the selective value of any individual character depends largely upon its relationship to the other characteristics of the plant.

NATURAL SELECTION AND THE ORIGIN OF FAMILIES AND ORDERS OF FLOWERING PLANTS

With this evidence in mind, we can now discuss the role of natural selection in guiding the major trends of evolution in the higher plants; that is, the origin of families and orders. In the present discussion, the writer will confine his attention to the flowering plants or angiosperms, since this is the group with which he is the most familiar.

Various botanists have stated that the differences between the modern families and orders of flowering plants have no adaptive significance, and so could not have originated under the guidance of natural selection. This statement even appears in one of the best known textbooks of elementary botany. In the remainder of the present discussion, evidence will be presented to support the writer's opinion that natural selection actually did play a dominant role in this important phase of plant evolution. In considering this evidence, two facts must be borne in mind. First, as pointed out in the last section, the adaptive significance is not the property of individual character differences, such as separate vs. united petals or superior vs. inferior ovary, but of harmonious combinations of characters. Second, the differentiation of most of these families and orders took place millions of years ago, probably in the Cretaceous period, when the world's fauna and flora were very different from those of modern times.

Two lines of evidence are available; the first from the study of the effect of specific agents of selection on particular character combinations, and the second from a survey of the distribution of different combinations of characters throughout the plant kingdom. The evidence already presented on methods of seed dispersal in the Gramineae and Compositae is an example of the first approach. An even better example is Grant's (1949) recent study of the relationship between pollinating agents of the flower and the type of character which is used to separate species and genera. This author cites several experiments which show that differences between closely related races or species in the structure of their flowers can cause pollinating insects to confine their visits to one type, as exemplified by the work of Mather (1947) on closely related species of *Antirrhinum.* This prevents or greatly restricts intercrossing, even when the two types grow intermingled in the same field. Such a hindrance will under many conditions be of selective value to both of the races concerned, since it will restrict the production of hybrids and their segregates, many of which are likely to represent disharmonious poorly adapted genotypes. Grant further points out that while many species of insects and birds are highly specific in their flower pollinating instincts, so that they tend to remain "faithful" to one species or race at least during a single pollen collecting excursion, other insects are quite indiscriminate in this respect. We

should expect that the groups pollinated by insects having flower constancy would contain a relatively large number of species and genera, and that they would be separated largely on the basis of characters of flower structure. This has been shown by Grant in two ways. First, in Southern California, a region noted for the richness of its fauna in flower constant bees, the mean number of species per genus in genera of bee-pollinated plants is 5.94, while in genera pollinated by non-constant, promiscuous insects the number is only 3.38. Second, a survey of the entire class of angiosperms has shown that in plants pollinated by bees and long-tongued flies, 40 per cent of the taxonomic characters pertain to the floral parts exclusive of the calyx, and 37 per cent of characters pertain to these organs in bird plants, but that the corresponding percentages are only 15 per cent in angiosperms pollinated by promiscuous insects, and 4 per cent in wind-pollinated groups. This shows that in many groups of angiosperms, the differentiation of species and genera has been guided to a large extent by natural selection in sorting out gene combinations which constitute different ways of adapting the species to cross pollination by animals. That the same was true also in past ages seems highly probable, although the animals which served as pollinating agents may have been different. We can also safely assume that in certain groups, particularly those adapted to impermanent or arid habitats, differentiation of species and genera has always been taking place on the basis of different methods of seed dispersal. Another reasonable assumption is that some of the species and genera which were first differentiated from each other in the Cretaceous period became the evolutionary lines which led to the modern families and orders. Therefore, the families and orders of flowering plants were probably differentiated from each other through the guidance of natural selection, which sorted out new mutations and preexisting gene differences relating to the reproductive parts into combinations adapted in various ways for cross pollination and seed dispersal.

A similar conclusion has been reached from the writer's survey of the different combinations of reproductive characters which distinguish the families and orders of angiosperms. This survey, which is presented elsewhere in more detail (Stebbins, in press), was made as follows. Based on the descriptions in various works, chiefly Hutchinson's (1926, 1934) *Families of Flowering Plants*, the 283 families were grouped according to their condition in respect to the eight characters most commonly used in the diagnostic keys to families. These characters are: (1) presence of both calyx and corolla vs. absence of one or both of these structures (dichlamydy vs. monochlamydy), (2) petals separate vs. united (choripetaly vs. sympetaly), (3) corolla regular vs. irregular (actinomorphy vs. zygomorphy), (4) stamens numerous vs. few (polystemony vs. oligostemony), (5) carpels separate vs. united (apocarpy vs. syncarpy), (6) ovules numerous vs. one or fewer per carpel (polyovuly vs. oligoovuly, (7) axial placentation vs. parietal, basal, or free central placentation, (8) ovary superior vs. inferior (hypogyny or perigyny vs. epigyny). In the above list, those conditions regarded by most botanists as the more primitive are mentioned first, and the more advanced ones second. On this basis, a particular group could be classified as primitive in all eight of the characteristics mentioned, as advanced in any one of the eight and primitive in the other seven, or as advanced in any combination of two, three, or more characters. A simple mathematical calculation will show that 256 combinations are possible.

When the families are classified according to the character combination which they represent, the first fact which appears most strikingly is that hardly any family is uniform for all of the eight characters. In other words, everyone of the major characteristics used to separate families and orders of flowering plants exists in some groups as a difference between genera of the same family or even between species of the same genus. This conclusion has great importance for future investigators in this field, since in certain groups the ecology and genetics of these character differences which normally separate families or orders can be studied on the level of species. The most variable family in this respect is the Saxifragaceae, even when taken in the narrow sense of Hutchinson. Study of the ecology, floral biology, genetics, and cytology of this family should be particularly rewarding in relation to the problem of the origin of higher categories.

The second and more important fact is that out of the 256 possible character combinations, only 79 are realized by any group, and of these, 30 are represented by only 1 or 2 families or part families. Furthermore, those combinations realized are represented very unequally. One combination is represented by 35 families or part families, which according to Hutchinson's classification are distributed through 17 orders, representing both

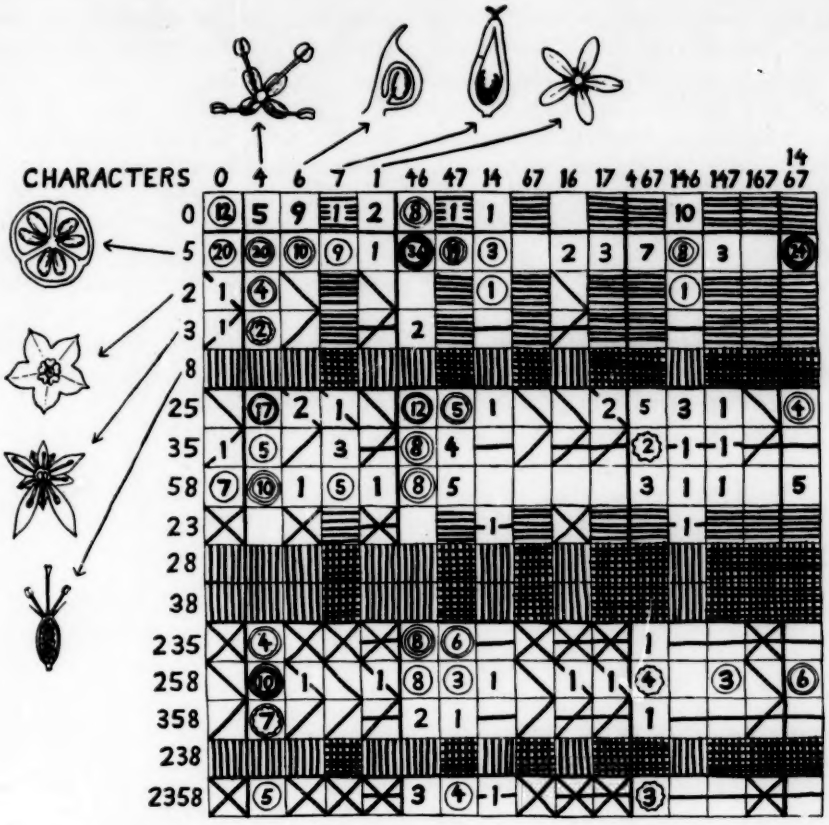

FIG. 3. Chart showing distribution of combinations of eight diagnostic characters among the families of angiosperms. Further explanation in the text.

monocotyledons and dicotyledons. And 203, or essentially half of the groups classified (because of the above mentioned variation within families, the number of groups is much larger than that of families) are contained in only 12 combinations, or less than 5 per cent of the total number possible.

Figure 3 shows the distribution of the 409 families or part families in the 256 possible character combinations. In this chart, each square represents the advanced condition in respect to the character or characters placed at the head of the vertical and of the horizontal columns leading to that square. The numbers within the square are the number of groups which have that combination of advanced characters represented by the square. Circles around the numbers indicate the presence of relatively large groups. Each thin line represents one group containing twenty or more genera, while each thick line represents five such groups. The five squares containing scalloped circles are each occupied by all or part of one of the four largest families of angiosperms (Gramineae, Orchidaceae, Leguminosae, Compositae), and therefore contain a group with two hundred or more genera. Most of the unoccupied squares are marked with a series of lines which indicate some structurally impossible or probably unadaptive combination of characters represented by that square. A more detailed discussion of this chart, togther with the complete list of family and part family groupings upon which it is based, will be presented elsewhere.

The most important question remaining to be considered is, does the arrangement of families and part families in this chart represent merely a chance set of groupings, or can the character combinations represented by a large number of groups or by a very large group be considered as adaptive "peaks" and the unoccupied or weakly represented character combinations as inadaptive "valleys."

Evidence in favor of the latter assumption can be obtained both from the characteristics of the groups found in the most strongly occupied squares, and from certain character combinations found in series of unoccupied squares.

For instance, of the 35 groups which have in common the characters dichlamydy, polypetaly, actinomorphy, oligostemony, syncarpy, few ovules, axial placentation, and hypogyny or perigyny (456 on the chart), 27 are woody, and most of these consist largely of shrubs to small trees, warm temperature to tropical in distribution. In contrast, the 10 groups with the set of advanced characters numbered 458 include 9 which are wholly or partly herbaceous, 6 of them being monocotyledons. While some of the groups having the same combination of characters are related to each other closely enough so that they probably originated from a common ancestor having these characteristics, this is certainly not true of all of them, and perhaps not even of the majority. This suggests that the combinations represented by many groups are adaptive "peaks" which have been "climbed" many times by different evolutionary lines, some of which have possessed similar vegetative characteristics or have lived in similar habitats.

Of the unoccupied squares, some represent combinations which are difficult or impossible to realize from the structural point of view. The principal ones of these are parietal placentation without syncarpy, found in the squares marked with a series of horizontal lines, and epigyny without syncarpy, marked with vertical lines. On the other hand, sympetaly without reduction of stamen member, marked with a diagonal line like this \, zygomorphy without reduction of stamen number, marked with the line /, and monochlamydy combined with zygomorphy, marked with a single horizontal line, are all structurally possible, but are represented by only a few groups. They are best interpreted as inadaptive "valleys." A more detailed analysis of other probable "peaks" and "valleys" will be presented elsewhere.

The conclusions from the evidence presented in this section are as follows. The various families and orders of angiosperms are characterized by combinations of a large number of characters, some of which (chiefly the eight shown in figure 3) are important differences between a large number of families of diverse relationships and represent parallel trends of evolution, while others are distinctive for particular families. Few if any of these characters have adaptive significance by themselves, but various combinations of them represent different ways of solving the all-important problems of cross fertilization and seed dispersal, and as such have a definite adaptive significance. The initiation of the evolutionary trends which led to the differentiation of orders and families may have been determined largely by the appearance of certain combinations of reproductive and vegetative characteristics in various races or species at least partly by chance, but the further evolutionary progress and differentiation of the successful families was guided chiefly by natural selection, taking advantage of the possibilities offered by the more favorable combinations. Although much further research along these lines is needed, there are now good grounds for the belief that natural selection is not only a real guiding force in the evolutionary adaptation of plants to different habitats, but that it has also played a prominent role in the much more complex process of the differentiation of higher categories on the basis of the characteristics of the reproductive system.

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SPECIATION AND SELECTION

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THE splitting of one species into several descendant species was, for a long time, one of the most puzzling biological problems. Darwin was rather vague on the subject, in fact he did not even make a clear-cut distinction between evolutionary change within a species and the multiplication of species. The evolutionary modification of a species in the course of time ("phyletic evolution" of Simpson) and the splitting of a mother species into several daughter species are two separate, although closely related, problems. The latter phenomenon, namely the multiplication of species, is always meant in the following pages whenever the term speciation is used.

Even though by 1920 the basic laws of inheritance had been well established by the geneticists, Bateson, the founder of British genetics, was forced to admit ignorance concerning the process of speciation (Bateson, 1922):

> When students of other sciences ask us what is now currently believed about the origin of species we have no clear answer to give. . . . That particular and essential bit of the theory of evolution which is concerned with the origin and nature of species remains utterly mysterious. . . . The production of an indubitably sterile hybrid from completely fertile parents, which have arisen under critical observation from a single common origin, is the event for which we wait.

We now know why Bateson and his contemporaries made no headway in elucidating the process of speciation. They were looking for the wrong thing because they had a mistaken species concept. Their thinking was unknowingly affected by a concept of idealistic philosophy. They were thinking of species as definite *types*, uniform within themselves, but separated from other species by an impressive morphological gap. The origin of such species would indeed be difficult to explain. It was this typological concept of species which induced de Vries to attribute the origin of new species to conspicuous major mutations. That this is not the solution of the species problem was, however, obvious to every naturalist.

The geneticists had found in the meantime that there were considerable genetic differences between individuals of sexually reproducing species and that, true to Darwin's prediction, the various genotypes differed in their selective value. In fact, Haldane and Fisher had calculated that even very slight differences of selective value would affect the genetic composition of the respective populations in due time. Geneticists had also found that the source of this genetic variability was random mutation.

Paleontologists and taxonomists (and biogeographers), on the other hand, had shown that the evolution of a new species was usually an exceedingly slow process, requiring a minimum of several hundred thousand years and averaging perhaps a million years or more. Furthermore, they had shown that this process was a gradual one, yielding no evidence of jumps. *Natura non facit saltum.*

Selection within living populations is something nearly instantaneous, operating anew during each generation, while speciation requires for its completion a time interval equivalent roughly to 30,000 human generations. To explain one in terms of the other would seem an even more difficult methodological problem than to explain the evolution of stellar galaxies by events and forces within atoms.

How it was possible to connect the almost instantaneous event of selection with the infinitely slow process of speciation shall be the theme of my discussion. The problem was solved by an elucidation of the nature of the speciation process.

The first step was a revision of the species concept. The old "type concept" of the species was founded on a morphological species definition based on the degree of difference between species. For reasons that have been stated elsewhere (Mayr, 1942, 1948) this species concept was replaced by a biological species concept founded on distinctness, measured in terms of reproductive isolation. In this concept, *a species is a group of interbreeding natural populations that are reproductively isolated from other such groups.* The subjective criterion of the degree of morphological difference has here been replaced

by the objective one of reproductive isolation, a criterion which has the additional advantage of selective significance.

Further work showed that reproductive isolation alone is not sufficient to permit coexistence of two species at the same locality. They also must be sufficiently different in their ecological requirements to avoid too severe a competition (Crombie, 1947).

If one knows these two essential attributes of species it becomes much easier to define speciation. Speciation then means the evolution of reproductive isolation as well as of ecological differentiation between populations. It will be our task to investigate to what extent selection is involved in the evolution of these species requirements.

THE STRUCTURE OF SPECIES

Decisive proof for the course of speciation comes from a study of the structure of species. It can be shown that species are not the uniform, homogeneous "types" which the typologists made them out to be. Rather, each species is composed of a great number of more or less differentiated populations. The knowledge of the geographical variability of species has greatly helped our understanding of the process of speciation. Each local environment exerts a continuous selection pressure against these local populations, and molds them thereby into adaptedness. That most species are polytypic in regard to morphological characters has long been known to taxonomists. That such local populations differ also by numerous adaptive features of habits, ecology, and physiology, and that these features have a genetic basis is a much more recent discovery.

The pioneer work in this field was done by Goldschmidt who showed in a series of papers summarized in 1934 that many of the characters of the Gypsy Moth (*Lymantria dispar*) vary geographically, including such physiological attributes as rate of growth, size, pigmentation, and strength of the sex genes. The most obviously adaptive character studied by him is the length of the incubation period. During the winter the young larvae undergo a diapause and stay enclosed in the egg. Even if the diapause is broken artificially and the eggs are exposed to a constant warm temperature, there is a lag of a certain number of days before the larvae hatch. The length of this "incubation period" depends on a considerable number of factors, such as the experimental temperature and the length of the preceding period of diapause. However, it is also closely correlated with the climatic characteristics of the place of origin of the eggs. In northern Europe and the northernmost island of Japan, where the vegetation develops very rapidly in spring after the long winter, the incubation period is short. In the Mediterranean, where the winters are warm but the vegetation is slow in spring, there is a very long incubation period, eighty-seven days at 11° C. against fifty-five days for central European eggs. The selective advantage of this accurate timing is obvious, since the larvae would die of starvation if induced by the warm winter weather of a Mediterranean country to hatch prior to the emergence of vegetation.

An impressive amount of similar evidence has accumulated since Goldschmidt's work confirming the thesis that each population of a species has been modified by selection to be adapted to the local environment. It would lead too far on this occasion to review this extensive literature covering both animals and plants. Only one more example shall be cited, the development of the Meadow Frog (*Rana pipiens*) (Moore, 1949). This species has a range that is much greater than that of any other North American frog, extending from Canada to Central America. There are pronounced climatic differences between various districts within this vast range, and this has led to the evolution of local populations which differ in their physiology. The most vulnerable period in the life cycle of these frogs is the embryonic stage between the fertilization of the egg and the metamorphosis of the young frog. It is in this stage that selection is most severe and it is in this stage that the greatest number of adaptive physiological differences between the various geographical races was found. Northern races (Quebec, Vermont, Wisconsin, New Jersey) and such from Louisiana tolerate a temperature low of 5° C. for normal development, while the lower limit is 9° for Ocala (Florida), 12.1° for Englewood (Florida), about 10° for Texas, and 12° for Mexico (Axtla). In turn, the southern populations were able to tolerate a higher temperature and still develop normally. The upper temperature limit for normal development in various populations was as follows: Quebec, Vermont, Wisconsin, and New Jersey 27.5°, Louisiana 32°, and Mexico (Axtla) 33°. At low temperatures northern frogs develop fast, e.g., at temperature 12° the number of hours required to reach embryological stage 20 (Moore,

1949) was as follows: Vermont 325, Louisiana 348, Florida (Ocala) 354, Florida (Englewood) 364, Texas 429, Mexico 396. There are additional adaptive differences in regard to egg size and shape of egg mass. It is evident from these data that the reason for the wide distribution of the meadow frog is its ability to become reconstructed genetically and to evolve genotypes that are adapted to the water conditions of the given region.

Numerous, usually much less well analyzed, examples of eco-geographical races in animals can be found in the literature (Mayr, 1942; Huxley, 1942).

NATURAL SELECTION IN LOCAL POPULATIONS

The simple fact that no two individuals (except identical twins) are alike in sexually reproducing species is too often ignored. One is willing to admit it for the human species and perhaps also for domestic animals, but all conspecific wild animals are commonly thought to be alike. To have proven that this is not the case is one of the major achievements of population genetics, foreshadowed by the population analysis undertaken by taxonomists. This variability includes not only the visible part of the genetic "spectrum," but also isoalleles and linked polygene systems. There appears to be an almost inexhaustible reservoir of gene combinations.

Even though much mortality in a population is due to accidents (rather than to lower fitness), there is unquestionably a greater probability that a superior (in selective qualities!) individual will reproduce than an inferior one. This will permit the rapid adaptation of a population to a local environment. It has been shown above that populations indeed are adapted to their local environment, but some more direct evidence shall be presented that this adaptation is due to selection.

NATURAL SELECTION UNDER EXPERIMENTAL CONDITIONS

As obvious as the effect of natural selection on adapted populations may be to the unprejudiced observer, irrefutable proof can be produced only by experiment. Such experiments proceed by two steps, both involving the raising of individuals from different natural populations under identical laboratory conditions. The first step consists in proving that indeed the two populations are genetically different by responding in a different manner to identical environmental conditions. The second step consists in proving that survival is affected by these conditions. This would show that these conditions have selective value and can change the genetic composition of the population.

VARIOUS SELECTIVE FACTORS

As a selective agent the environment always acts as a whole. Sometimes it is possible to single out a specific factor and to indicate what role it plays in determining the genetic composition of a local population. Heuts (1947, 1948) has shown this for the effect of salt water and temperature on the Three-spined Stickleback (*Gasterosteus aculeatus*). In this species there are populations (type B) with a high number of plates on the sides of the body, which live mainly in coastal waters of high salinity, and inland populations (type A) with low plate number which live in fresh water. It was shown, as is to be expected, that in salt water there was a high percentage of hatching and survival of young of the salt-water race and low survival of individuals of the fresh-water race, while in fresh water the survival of the two races was reversed. Also there was very different survival of the different strains when raised at different temperatures.

The extensive work of Goldschmidt on *Lymantria dispar* has already been referred to above. It showed that numerous physiological characteristics of geographical races of this species have a genetic basis and in many cases it could be shown that larvae from different regions have different survival when raised under identical conditions. For additional evidence of differential survival of races of the same species see, among others, Speyer (1938), Basinger and Smith (1946), and Albonico (1948). What effect a particular factor has depends sometimes on a constellation of circumstances. Schüz (1942) showed for the White Stork (*Ciconia ciconia*) that the least mortality of young occurred in northwestern Germany during dry springs and in Hungary during wet springs.

Biotic factors of the environment are sometimes as efficient selective agents as climate or some other general factor of the environment. Armstrong (1945) showed that in a large, rather isolated pear orchard in southern Ontario a local race of the codling moth (*Carpocapsa pomonella*) had evolved which emerged two to three weeks later than the codling moth populations in apple orchards. This late emergence coincided with the softening of the ripening pears while young pears

have a stone layer under the epidermis which makes them impenetrable to these larvae.

Many species of insects are monophagous, that is they feed on a single species of host plant. The strong selective effect of the host plant becomes apparent when it is possible to shift individuals of such a monophagous species artificially to a new food plant. Chrysomelid beetles (*Gastroidea viridula*) that normally feed on sorrel (*Rumex*) had to be bred for two generations on knotweed (*Polygonum*) before they were adapted to the new food plant. During the first generation, while being submitted to forced feeding, nearly half the individuals died (*Kozhantshikov*, 1941). Adaptation to a specific food plant is obviously subject to severe selection.

One of the reasons why biotic factors often are such important selective agents is competition. Although the effect of competition had been postulated already by Darwin and was vaguely suspected ever since, it has been fully demonstrated only rather recently. If two closely related species of flour beetles, *Tribolium castaneum* and *T. confusum*, are brought together in a single homogeneous food medium, either one or the other species will be wiped out. *T. castaneum* usually becomes exterminated in cultures that are infected by the sporozoit *Adelina tribolii*, while *confusum* is usually the one that dies out in uninfected cultures (Park, 1948). In nature both species are widespread and prosperous, presumably because they are able to select slightly different niches and thus avoid fatal competition. It would seem superfluous to say anything more on the selective effects of competition since there is an excellent recent review on the subject (Crombie, 1947).

THE SEVERITY OF SELECTION

How quickly some genes respond to selection has been indicated in a number of recent papers although only part of the evidence is available in all these cases. The application of insecticides has resulted in an amazingly rapid evolution of highly resistant strains in many species of insects (Quayle, 1943). Very high selection coefficient have been made probable by Goldschmidt (1948) for the genes that produce industrial melanism in certain moths.

The new study of gene arrangements in *Drosophila* has the great advantage that genotypes are studied rather than phenotypes, although unfortunately it is unknown how many genes are situated on the inverted chromosome sections. Dobzhansky (1947, 1948*a*, *b*) for *Drosophila pseudoobscura* and Dubinin and co-workers for *D. funebris* (1946*a*, *b*) have shown that definite frequencies of certain gene arrangements have specific survival values. This became apparent from their distribution in nature and was corroborated by a study of experimental laboratory cultures.

CONCLUSIONS

Whenever and whatever tested, it has been shown that every population of a species is adapted to the conditions of the respective local environment. Furthermore, it has been shown that this adaptation is due to a balance of genetic factors which is often so delicate that it may respond to the seasonal and annual changes of the environment. Finally, these seasonal changes as well as the differences between populations are caused by selection.

The botanists have gathered an equally or even more impressive body of evidence in favor of these conclusions than the zoologists.

So overwhelming has the evidence become that these conclusions are not even denied by those, who, like Goldschmidt (1940), postulate evolution by large jumps, by macromutations or systemic mutations. The adaptation of local population and its causation by selection can be considered a fact.

THE BREAKING OF THE SPECIES BOND

If a species is as plastic as has been depicted, it is perhaps even more puzzling how it can split into several species. Perhaps a species is like a toy figure made of rubber which can be pulled into all sorts of shapes without losing its cohesion. This is indeed what Goldschmidt claims. According to him the local populations of a species are not incipient species. He believes that no amount of selective molding by the environment can change a population of a species into a new species.

To me it seems that all the available evidence indicates just the opposite. New species arise from isolated and much modified portions of parental species. The full evidence for this assertion has been given elsewhere (Mayr, 1942: 147–185). Only a summary can be given on this occasion. The most convincing proofs are these:

(1) The geographical subspecies studied by the taxonomist are often of the same kind as the

temporal subspecies studied by the paleontologist in successive strata. Since it has been possible in many cases to demonstrate the transformation of temporal subspecies into species, there is no reason to assume that geographical races should not do likewise if the circumstances are favorable.

(2) The distinctness of species is maintained by isolating mechanisms (Dobzhansky, 1941). To explain speciation it is necessary to explain the origin of these isolating mechanisms. If isolated populations of species are incipient species they also must have incipient isolating mechanisms. This indeed has been shown in an ever increasing number of cases. Frequently there is reduced fertility or almost complete sterility between geographically distant populations of the same species. Reduced fertility or partial ethological isolation has been found in many species of *Drosophila* and Lepidoptera (Mayr, 1948). Moore (1946) found much hybrid inviability between distant populations of the frog *Rana pipiens*. The voice, the courtship organs, and the structure of the genital armatures vary geographically in many species of animals. The Indian and European honey-bees (*Apis indica* and *A. mellifica*) are reported not to be crossable even though linked by a series of intergrading populations (Goetze and Schmidt, 1942). A similar geographical variability is shown by habitat preference, food plant preference, season of reproduction, and all the many other factors of which isolating mechanisms are composed. The picture presented by the geographical variation of isolating mechanisms is fully consistent with the theory of geographical speciation.

(3) There is hardly a genus of animals which does not contain some incipient species or borderline cases. In many species, there are isolated, peripheral populations that are so distinct that they could be classified with equal justification as species or subspecies. There are the so-called superspecies, groups of allopatric species, which reveal through their distribution pattern that they are the products of geographical speciation. There are the multiple invasions of islands which prove that during isolation a population can reach species level. Finally, there is an ever increasing number of rings of races known in which the terminal links overlap without interbreeding while there is complete interbreeding between the adjacent populations of which the ring is composed. The existing number of such borderline cases is far in excess of the number needed to replace those species that appear to be vanishing. More convincing proof for geographic speciation can hardly be expected.

SELECTION AFTER SECONDARY OVERLAP

Selection not only starts speciation by causing genetic divergence of originally similar populations, selection also completes speciation. Species require two attributes in order to coexist successfully side by side, reproductive isolation and ecological compatibility. These attributes are acquired by isolated populations only incidentally, namely as by-products of the general genetic divergence occurring during isolation.

When such populations come together again secondarily, any one of three things may happen. Either they have not acquired reproductive isolation, then the formation of a "hybrid" zone will occur, or else they have acquired reproductive isolation but not ecological compatibility. The result will be a meeting of the two species along a sharply defined border without any noticeable overlap.

Finally, they may acquire both prerequisites and if this condition is fulfilled the last obstacle is removed from a wide mutual overlapping of their ranges. However, since both species are not "types" in the sense of the natural philosophers but variable populations, they may and usually will contain individuals that are either not completely reproductively isolated or not completely compatible ecologically. Here again selection sets in. The ecologically incompatible individuals will be at an obvious disadvantage. This is equally true for individuals that are not reproductively isolated for they will produce hybrids, and hybrids are nearly always of lower fitness and their genes will be eliminated. The result will be greater survival of the individuals with well developed isolating mechanisms and hence a steady improvement of these mechanisms. There is some evidence that this is not pure theory. Dobzhansky (1941) found that there was a greater amount of isolation between *Drosophila miranda* on one hand and both *D. persimilis* and *D. pseudoobscura* if populations of the latter two species were used that came from the area of overlap. King (1947) found that among three very closely related species of *Drosophila,* the two species which occurred sympatrically in Brazil, *D. guarú* and *D. guarani,* were completely isolated sexually. The two species, however, interbred fairly freely with an allopatric third species, *D. subbadia,* which is known only from Mexico. An improvement of isolating mechanisms in

zones of overlap was also found in *Triturus* (Lantz, 1947).

Evidence for the selective effect of competition on ecological species differences has been presented by Lack (1947) for the Galapagos Finches and by Amadon (1947) for the birds of the Hawaiian Islands.

SUMMARY

Geographical speciation is the normal process by which species multiply. Isolating mechanisms are formed as a consequence of the genetic divergence of populations, while they are protected by extrinsic barriers against disturbing gene flow from other populations of the parental species.

Natural selection is effective at three stages of the speciation process,

(1) it continually molds all the populations of a species to be adapted to their local environment,

(2) it remodels isolated portions of a species while they are protected against gene flow from the main body of the species,

(3) it perfects isolating mechanisms after the two populations have reestablished contact and eliminates individuals with imperfect isolating mechanisms. Likewise, it tends to eliminate individuals that are closest to other sympatric species in their ecological requirements.

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